Megaherbivores and the Maintenance of Biodiversity

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ABSTRACT

Due to alarming rates of wildlife decline throughout the world, ecological monitoring programs have become a critical component in evidence-based conservation planning. Continuous systematic monitoring using standardized camera trap grids helps to detect trends in wildlife population dynamics; however, the amount of data generated can be difficult to process in a timely manner. To mitigate this issue, citizen science and cutting-edge machine learning technologies can be combined to accelerate data collection, analysis, and reporting. In this dissertation, I will describe the creation, goals, and outcomes thus far of the Snapshot Safari project, an international, long-term ecological monitoring network using ~2000 camera traps and a hybrid data classification pipeline. Next, I'll demonstrate the general utility of Relative Abundance Indices (RAIs) from camera trap data collected at five South African protected areas of varying sizes, management types, and herbivore assemblages by comparing them to RAIs from aerial surveys that were conducted during the same period. Finally, I will discuss the 'elephant problem' in South Africa and draw on three decades of long-term transect data on woody plant species combined with aerial surveys to examine the effects elephants exert on their ecological communities and, consequently, biodiversity at multiple trophic levels when they recolonize an area after extirpation.

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Chapter 1

Snapshot Safari: Long-term biodiversity monitoring to assess wildlife population dynamics

with Craig Packer, Lain E. Pardo, Jan A. Venter, Michael J. Somers, Hervé Fritz, Colleen Downs, Abby Guthmann, Robyn Hetem, Mark Keith, David S. Jachowski, Aliza le Roux, Nokubonga Mgqatsa, Meredith S. Palmer, Daniel M. Parker, Mike J.S. Peel, Rob Slotow, W. Maartin Strauss, Lourens Swanepoel, Craig Tambling, Nairobi Tsie, Mika Vermeulen, and Marco Willi

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ABSTRACT

Due to alarming rates of wildlife decline throughout the world, ecological monitoring programs have become a critical component in evidence-based conservation planning. Continuous systematic monitoring using camera trap grids helps to detect trends in various biodiversity indicators. However, the amount of data generated can be difficult to process in a timely manner. To mitigate this issue, citizen science and cutting-edge machine learning technologies can be combined to hasten the rate of data collection and analysis to assess the conservation status of threatened species. Here, we introduce the Snapshot Safari project, an international, large-scale camera trap monitoring network that produces data to study the diversity and ecological dynamics of southern African mammals and to inform conservation planning in protected areas. The data pipeline incorporates a citizen science cohort of thousands-strong with machine learning algorithms trained to identify African wildlife species. Distributed management allows researchers to focus on local issues while collecting data in a standardized manner to facilitate cross-site comparisons of new and existing conservation programs at multiple scales. We emphasize the importance of developing long-term, sustainable monitoring projects for Africa and other parts of the world experiencing high rates of species extinctions. We further discuss the potential to advance automated camera trap image processing techniques and the importance of public support in monitoring programs.

INTRODUCTION

Nature is experiencing degradation and extinction rates that are unprecedented within human history.[1,2] Consequently, continuous large-scale monitoring programs are critical to provide insights into population trends and to aid in understanding factors associated with altering population dynamics at various temporal and spatial scales.[3] Continuous monitoring is important not only for tracking rare or threatened species but also to detect the increase of potentially invasive species[4], and the trends in the populations of common species, which in some regions are declining even more rapidly than are rare species.[2]

Many countries have committed to reducing biodiversity loss through voluntary international agreements (e.g., Aichi Biodiversity Targets, United Nations Sustainable Development goals, Paris agreement). To meet these targets, managers of protected areas and other stakeholders need reliable data on wildlife distributions, abundance, and ecological interactions across habitats, biomes, and management systems. Continuous large-scale, long-term monitoring programs are critical to obtain baseline population levels, provide insights into population trends, and advance knowledge of the factors associated with altered population dynamics at various scales[5]. Continuous monitoring is important not only in tracking rare or threatened species but also trends in common species populations. This includes monitoring increases in invasive species, which can disturb the autoregulation of natural systems. Due to the rapid extinction rates of rare species, downward trends in common species are often overlooked but, in some regions, they are declining more rapidly than rare species[6,7].

Monitoring of ecosystems and the species that inhabit them is especially relevant in Africa – a highly biodiverse continent with numerous iconic mammal species threatened by human activities, e.g., poaching and human-induced climate and land use change[8]. Over half of the terrestrial mammals in Africa have experienced range contractions of as much as 80%, on average, including predator species such as lions (*Panthera leo*) and large herbivores that are important components of healthy ecosystems[2]. However, data that inform conservation status assessments of many species is outdated and limited to single species or orders. Many areas in Africa, therefore, lack the baseline biodiversity data necessary to assess the outcomes of existing conservation programs[9]. Further, the lack of standardized methods to assess biodiversity patterns hampers our ability to detect and respond to changes in mammal populations caused by environmental and anthropogenic factors. The importance of advances in technological monitoring has been highlighted by the United Nations Environment Program (UNEP) through the proposed "Digital Ecosystem framework", a complex distributed network or interconnected socio-technological system.[10]

To systematically map biodiversity, monitor ecological dynamics of African mammals, and evaluate conservation outcomes, we have formed a collaborative network, Snapshot Safari (www.snapshotsafari.org). This network (hereafter Snapshot) comprises a multinational collective of ecologists, wildlife managers, citizen scientists, computer scientists, local community members, and other academics and conservationists working together to conserve and restore African mammals. Snapshot has deployed camera trap grids in Botswana, Kenya, Mozambique, South Africa, Tanzania, and Zimbabwe using standardized camera trapping protocols. We plan to run these grids continuously for a decade or more to assess population trends in response to human perturbations and environmental changes. To facilitate efficient image processing, we have combined citizen science efforts with advanced machine learning techniques[11]. Here, we introduce the Snapshot network and highlight biodiversity mapping and conservation efforts in South Africa as a model system.

1. Snapshot Safari

1.1 Collaborative Network

Snapshot is one of the largest ecological monitoring networks in the world (But see TEAM Network, eMammal, Snapshot USA). It began with a single camera trap grid in Serengeti National Park, Tanzania in 2010 and a flagship citizen science project dubbed Snapshot Serengeti[12]. Within three days of Snapshot Serengeti's online launch in 2012, volunteers contributed over 1 million classifications and quickly cleared the entire backlog of images. The data produced by the cameras running continuously in the

Serengeti provides the basis for papers on spatiotemporal partitioning[13–15]; behavioral interactions[16,17]; and advancing modeling techniques used on camera trap data[18,19]. The millions of images generated annually by the Serengeti grid have been utilized as training data for deep learning algorithms developed to automatically identify African mammal species[11,20,21].

Recognizing the difficulty in comparing Serengeti data to camera trap images collected elsewhere, the team at University of Minnesota Lion Center reached out to colleagues working in other African parks and universities to gauge interest in collaborating to expand the protocols systematically. The original Snapshot model has since been deployed in 44 additional parks and nature reserves in six countries: Botswana, Kenya, Mozambique, South Africa, Tanzania, and Zimbabwe (Figure 1.1). Participating locations represent a variety of habitats, wildlife communities, management types, protected area sizes, and grid sizes. Camera traps are deployed in grids at every site using the standardized protocols as described below. Metadata on camera placements and habitat characteristics are also collected in a standardized manner to facilitate cross-site comparisons.

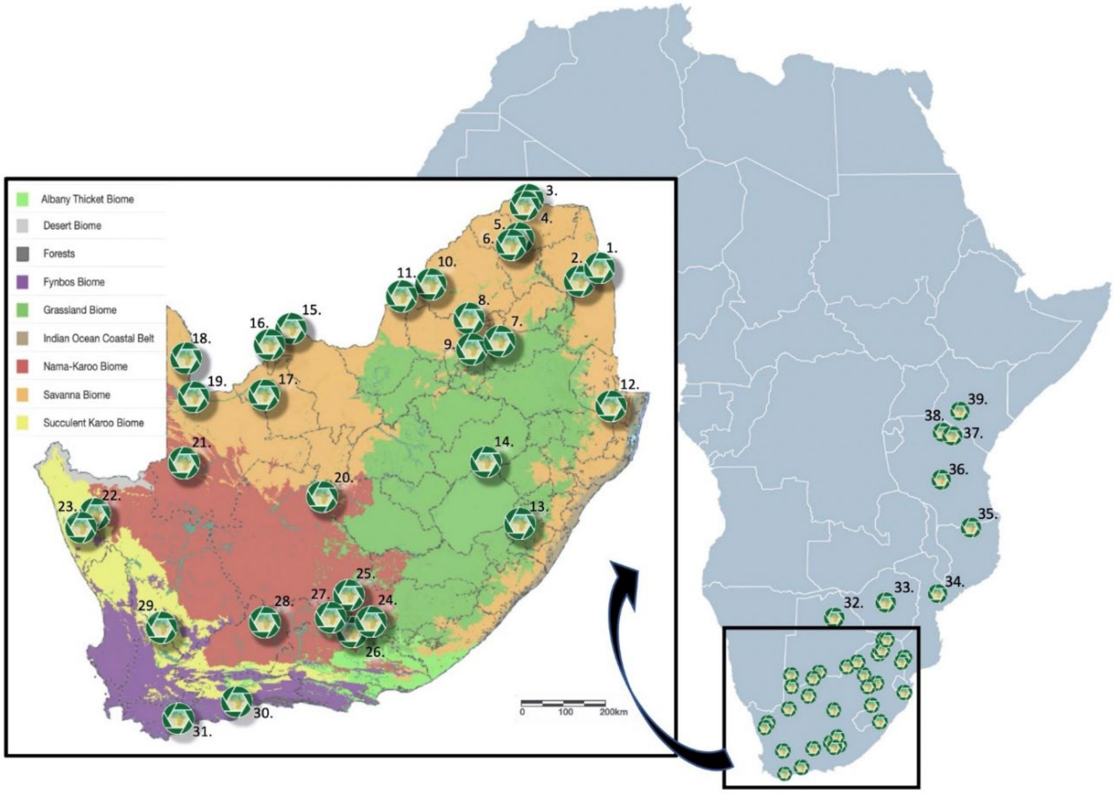

Figure 1.1. Permanent Snapshot Safari study locations as of 2020.

1. Kruger National Park **2.** Associated Private Nature Reserves **3.** Mapungubwe Nature Reserve **4.** Venetia Nature Reserve **5.** Lanjan Nature Reserve **6.** Blouberg Nature Reserve **7.** Telperion Private Nature Reserve **8.** Pilanesberg National Park **9.** Rietvlei Nature Reserve **10.** Atherstone Nature Reserve **11.** Madikwe Game Reserve **12.** Somkhanda Game Reserve **13.** Ntsikeni Wildlife Reserve **14**. Golden Gate Highlands National Park **15.** Khamab Kalahari Game Reserve **16.** Molopo Nature Reserve **17**. Tswalu Kalahari Reserve **18.** Kgalagadi Transfrontier Park **19.** Khomani San Common Property Association **20.** Mokala National Park **21.** Augrabies Falls National Park **22.** Goegap Nature Reserve **23.** Namaqua National Park **24.** Mountain Zebra National Park **25.** Bergplaas Nature Reserve **26.** Samara Private Nature Reserve & De Nuk Farm **27.** Camdeboo National Park **28.** Karoo National Park **29.** Tankwa Karoo National Park **30.** Gondwana Game Reserve **31.** DeHoop Nature Reserve and Overberg **32.** Makgadikgadi Pans National Park, Botswana **33.** Debshan Ranch, Zimbabwe **34**. Gorongosa National Park, Mozambique **35.** Niassa National Park, Mozambique **36.** Ruaha National Park, Tanzania **37.** Serengeti National Park, Tanzania **38.** Grumeti Game Reserve, Tanzania **39.** Enonkishu Conservancy, Kenya

1.2 Standardized Methods

a. Field Surveys

Snapshot camera trap grids consist of regularly spaced cells of 5 km^2. Deployment teams select trees facing game trails within 250 m of the computer-generated grid point coordinates for each camera or install poles where trees are not available. Cameras housed in steel cases are hung at heights of about 50 cm, ideal for capturing most medium- to large-bodied mammals[22]. Each camera is programmed to take a series of three images within 10 seconds of each other (a ‘capture event’) when passive infrared (PIR) sensors are triggered by motion or heat during the day (set for a one-minute time lapse between captures) and a single image at night to save battery power[12]. Most grids have operated continuously for at least four years and are intended to run for a decade or longer. This structure facilitates systematic coverage when monitoring multiple species[23,24] and captures most mammal species >1 kg at each site. We use a variety of cameras across projects, but most are Cuddeback® Professional models in black or white flash depending on the guidance of the reserve (Cuddeback, Wisconsin, USA). SD cards and rechargeable batteries are changed every 8-10 weeks. Data collected are forwarded to the University of Minnesota Lion Center for curation and management of the citizen science component.

b. Citizen Science

To classify millions of images generated annually and to spread public awareness about African species, Snapshot partners with the citizen science platform Zooniverse.org. Citizen scientists (volunteers who wish to participate in meaningful research experiences) access Zooniverse either through a browser or a mobile app. In the first phase, Snapshot volunteers remove blank images; in the second phase, they identify species, count the number of individuals, record behaviors, and note the presence/absence of young. Volunteers can toggle between images in capture events, animate the sequence to facilitate the identification of small or distant animals, and interact directly with researchers on the talk boards or via social media. Each project has its own webpage within the Snapshot organization—25 to date, with some adjacent small reserves grouped into a single project—highlighting local conservation, research, and outreach programs, as well as the unique characteristics of the park's wildlife and geographic features. More than 200,000 volunteers worldwide have contributed their time to classify >12 million photos since the relaunch of Snapshot as a network in February 2018.

For the original Serengeti grid, 5-25 volunteers were required to reach a consensus at an appropriate level of accuracy. The consensus responses exhibited 97% accuracy compared to expert assessments, confirming the reliability of citizen science in rapidly processing large volumes of data[16]. However, the addition of many new sites strains volunteers' ability to keep up with the millions of images captured annually across Snapshot sites. The current citizen science interface employed by Snapshot is similar in process, but the requisite human effort is significantly reduced by the introduction of machine learning algorithms.

c. Machine Learning

The Snapshot network incorporates machine learning algorithms prior to uploading data to Zooniverse to decrease the number of citizen scientists required to view each capture event[11]. Two image classifiers (convolutional neural networks) are employed: one to identify empty images and one to predict the species, counts, and behaviors in images containing wildlife. The algorithm's predictions and confidence levels are uploaded and used to Zooniverse with the image manifest and used to dynamically determine the level of agreement and number of volunteers required to confirm the algorithms' label (Figure 1.2). The millions of images generated annually by the Serengeti grid have been utilized as training data for many deep learning algorithms developed to identify African mammal species automatically[11,21,25].

The first stage of classification occurs on the Zooniverse in a binary workflow, in which volunteers are asked to evaluate whether animals can be seen in the images. If two people agree with the algorithms that an image is empty, it is retired from the dataset. If one of the first two people disagrees with the computer, the image will remain in circulation to accumulate three more human votes at which point the majority consensus is accepted. Images marked as containing wildlife are moved to the second stage of classification, in which the species, count, and behaviors are annotated. At this stage, dynamic retirement rules within the Zooniverse infrastructure are used to retire captures based on the species, agreement of the volunteers with the computer and one another, and the algorithm's confidence in its own prediction.

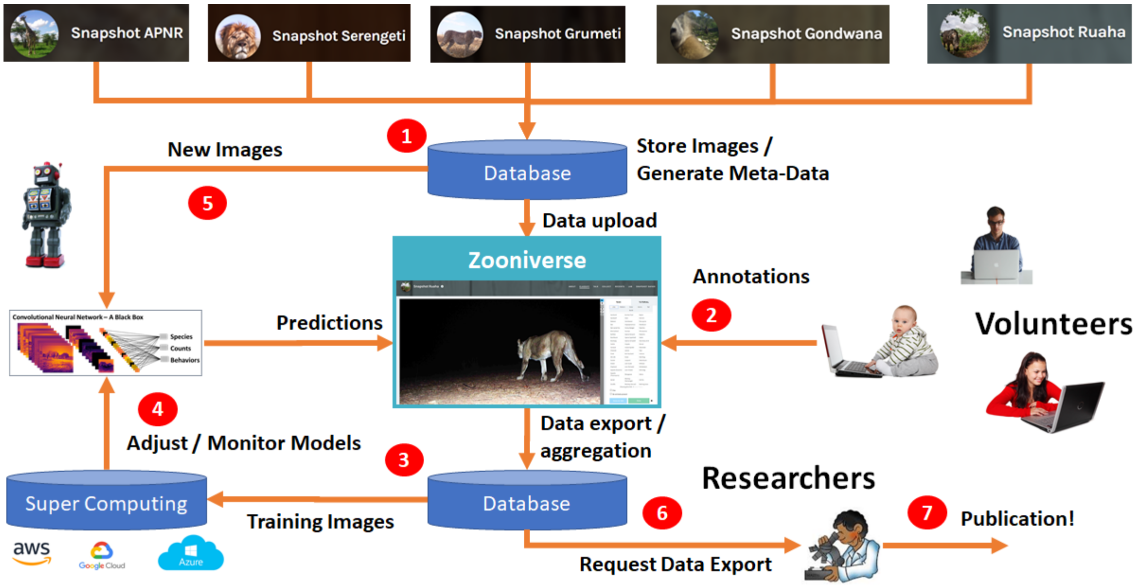

Figure 1.2: Snapshot Safari data processing workflow. **(1)** Data from each location is checked for errors (bad flash, date-time reset) and run through machine learning algorithms during the pre-processing phase. **(2)** Data and machine learning predictions are uploaded to Zooniverse for classification. Every image is classified by multiple volunteers, and their votes are aggregated to assign labels of species, count, and behaviors. **(3–5)** Citizen scientists' labeled annotations are used to iteratively train and refine the machine learning algorithm. **(6–7)** Data are returned to researchers and reserve management for publications and conservation assessments.

As a result of quickly removing blank images and those of humans and common species, citizen scientists are presented with more images of rare and cryptic species, improving the volunteer experience[26] and providing valuable data to refine machine learning algorithms' capabilities. This has improved efficiency by 43% thus far Snapshot Serengeti images[11]. The citizen science and machine learning stages are applied iteratively to constantly improve performance and efficiency. Labeled images from all projects are used to retrain new and existing models to improve the machine's predictive capability in a variety of habitats, and the refined model is run on new datasets as they are collected from the field (Figure 1.2).

1.3 International effort, local results

Snapshot is documenting the presence, distribution, diversity, and ecology of 85+ African mammals. The variety of Snapshot locations provides numerous opportunities to answer challenging questions in wildlife ecology and conservation, test ecological hypotheses and analytical methods, and measure the impacts of anthropogenic disturbances across multiple spatiotemporal scales. For example, the data produced by the camera traps running continuously in the Serengeti provided the basis for papers on spatiotemporal partitioning[15-17], behavioral interactions[18-20], and advancing modelling techniques used with the camera trap data[11,19,21].

The distributed management of Snapshot grids has direct positive consequences for conservation management because scientists visit sites regularly to maintain and manage the camera trap grids as well as to improve rapport with neighboring communities. This helps scientists align grid management with locally relevant research and conservation goals. For example, Golden Gate Highlands National Park has been able to assess the effectiveness of existing vulture conservation efforts. In the Kalahari, researchers are building strong relationships with local communities like the Khomani San, who use the camera trap information to improve their wildlife management practices. In Ruaha National Park, Tanzania, researchers trained community members to deploy and maintain the grid, creating conservation jobs and infrastructure[27]. Though education, outreach, and information are accessible to anybody with an internet connection in the modern era, in practice, place-based connections and positive collaborations between scientists and residents are necessary to sustain research and conservation efforts.

2. Snapshot Safari – South Africa

Like other African countries, South Africa lacks adequate conservation data for many species, and about 17% of mammal species are threatened with extinction.[8] However, South Africa has a long history of conservation interventions and is, therefore, a testing ground for different hypotheses. In South Africa, we have surveyed 31 locations (Figure 1), of which 21 are permanent grids for long-term monitoring purposes. These represent a total of 1,408 cameras deployed for grids on permanent locations and 873 installed in the roaming locations.

Our grids and collaborative research allow us to combine different questions and leverage the full potential of camera traps. For example, in the Kruger National Park we have set up the cameras along with studies of the phenology of vegetation cover (e.g., tree and herbaceous composition, cover and structure), which has created an opportunity to monitor the vegetation dynamic while accounting for mammal presence. Further, by-catch data (not targeted species), such as birds and human activity, will represent an interesting opportunity to investigate other species in the future. The potential role of this by-catch data of camera trap studies to conservation efforts or ecological studies has recently been highlighted[28].

Our grids have documented sightings of some threatened and elusive species outside known distribution ranges, as well as unusual behavioral interactions. We observed leopard (*Panthera pardus*) in Karoo National Park in June 2018 with another observation in August 2019 confirming residence. This new record is the first sighting of leopard in the region since their extermination more than 200 years ago (Figure 1.3A). The second record of interest was that of brown hyaena (*Hyaene brunnea*) in Camdeboo National Park (near Graaf Reinette, Eastern Cape) in April 2019 with two more later records in November and December 2019 (Figure 1.3B). Both sightings were unexpected and represent significant range shifts for these species. In June 2019 in the Karoo National Park, one of the Snapshot cameras took 21 pictures of three to five meerkats (*Suricata suricatta*) and a yellow mongoose (*Cynictis penicillata*) foraging together and sharing vigilance (Figure 1.3C). These observations constitute new evidence to support the only previous observation of this cooperative behavior in the Andries Vosloo Kudu Nature Reserve in the Eastern Cape Province.[24]

Figure 1.3. Examples of unexpected species distributions and behaviors captured by Snapshot Safari cameras. A) First sighting of a leopard at Karoo National Park in 200+ years. B) First sighting of a brown hyaena in Camdeboo National Park. C: A yellow mongoose (foreground) foraging and sharing vigilance with a band of meerkats at Karoo National Park.

Systematic long-term monitoring is crucial to understand trends in populations and species through time and to facilitate informed management decisions. However, data collection via camera traps has increased at a much faster rate than have our technical capabilities to analyze such large data sets[29] Another limitation is the access to research groups and computational centers with sufficient processing infrastructure to train and run machine learning algorithms. In our project, for example, the information is analyzed by the Lion Center at the University of Minnesota. All data are sent to that lab group for the management of the online classification process and data curation. This can create a bottleneck and slow the data pipeline. One potential solution is to set up multiple hubs within a network, which we plan to enact by copying existing infrastructure onto South Africa’s supercomputer at the Centre for High Performance Computing. This continues the trend of distributed management and provides additional opportunities for training and professional development.

Snapshot also provides helpful data for computer scientists who wish to build artificial intelligence algorithms to automatically identify wildlife species without human assistance. Data from six South African sites (and the Serengeti) is publicly available for download on the Microsoft-hosted site Labeled Image Library of Alexandria – Biology &

Conservation (LILA-BC) at lila.science. More data is added to the labeled image repository as datasets are finalized. In all cases, images of humans and rhinos are withheld from the repository for privacy and poaching concerns, respectively. Metadata on habitat and environmental characteristics are available to researchers outside of the network upon request. This ensures that local researchers and reserve management are aware of how the data are being used and have the opportunity to contribute and collaborate.

We aim to be as collaborative as possible and share data to facilitate other conservation and research projects as well. For example, we have shared records with the MammalMAP initiative, which provides a platform for citizen scientists and researchers to contribute biodiversity information for South Africa (http://vmus.adu.org.za/). We have shared data available with other platforms such as the Foundational Biodiversity Information Programme in South Africa (http://fbip. co.za/) and the Global Biodiversity Information Facility to help evaluate progress toward governmental agreements like the UN Sustainable Development Goals. Our data has also been formatted to share with the Darwin Core (https://dwc.tdwg.org/). Evaluating trends at the broad geographic scale of the Snapshot network could inform IUCN Red List entries on species for which we currently lack accurate estimates of extant population sizes.

3. Future directions and conclusions

The Snapshot collaborators in South Africa meet annually to review current projects, prioritize future research, and plan funding activities. We anticipate that the data collected from this initiative will be used to address diverse research priorities in conservation and wildlife management and will increase understanding of ecological process mediated by southern African mammals. As such, we have defined five overarching research themes, each with specific questions that are currently in process and others intended to guide biodiversity research at various institutions, especially those that are part of our partnership.

> **Theme 1:** The role of anthropogenic landscapes in shaping biodiversity, distributions, populations, and communities.

Theme 2: Investigating ecological interactions and food webs through space and time.

Theme 3: Understanding and predicting the consequences of climate change for mammal behavior, distribution, adaptation, and community composition.

Theme 4: Assessment of conservation priorities and protected area effectiveness.

Theme 5: Merging camera trap data with other data to address more specific questions and improve monitoring.

The planet and most of its biodiversity is rapidly approaching a tipping point[30]. It is therefore imperative to provide meaningful and timely assessments of the status of biodiversity and ecological processes at conservation-relevant scales. Snapshot's integration of scientists, citizens, and technology can play a valuable role in achieving this goal. Our collaboration holds great potential to contribute to the advancement of statistical and technological capacity in South Africa and other African countries. Snapshot grids provide valuable data to advance scientific inquiry across a variety of ecosystems and to systematically assess biodiversity trends in some of Africa's most ecologically diverse regions. Such data are critical to creating productive and resilient conservation policies in these global biodiversity hotspots.

Harnessing technology to build a 'Digital Ecosystem' is indeed a fundamental way to keep track of the state of biodiversity and evaluate global commitments. Empowering citizens with technology to help collect the necessary evidence of the severity of the global environmental crisis and assist scientist and stakeholders to monitor the impact of their decisions benefits all parties. With the current advances in data processing, we are hopeful that Snapshot will provide timely recommendations and data for mammalian species that would make conservation accountable and adaptable to changes in southern Africa. At the beginning of the 'Climate Century', Snapshot Safari is poised to generate unprecedented levels of standardized data that will be used to monitor and protect

African wildlife while simultaneously educating the public about the importance of large mammals and their cascading effects on the maintenance of biodiversity and ecosystem stability. However, only political will and multi-sectoral commitments will make it possible to leverage the potential of technology to produce practical effects.

Chapter 2

Assessing the reliability of Relative Abundance Indices drawn from camera traps vs. aerial surveys across diverse African landscapes

with Craig Packer

ABSTRACT

Accurately estimating population sizes of free-roaming wildlife is a challenge in most terrestrial ecosystems, yet it is of paramount importance for conservation planning and management. Camera traps are a popular and widely used method of continuously collecting observations of mammals, but aerial surveys are considered the most accurate method of population census over large areas. In this paper, we test the general utility of RAIs in estimating the population sizes of 24 herbivore species across five South African nature reserves and analyze a series of factors that might be expected to cause CT grids to either over- or under-estimate population sizes relative to aerial surveys. We use data collected by the Snapshot Safari program to compare RAIs calculated from CT images at South African PAs of varying sizes, management types, and wildlife assemblages against RAIs from aerial surveys that were conducted during the same period. Even with continuously collected data, abundance estimates drawn from camera traps are not comparable to estimates from aerial surveys and the two methods do not produce the same trends from year to year. While camera traps have produced valuable estimates of species richness, density, occupancy, and activity budgets, their power to accurately estimate species abundance and density remains a topic of debate.

I. INTRODUCTION

Due to widespread losses in biodiversity[31] and the accelerating knock-on effects of climate change and habitat conversion[32], landscape-level ecological monitoring is imperative for the successful conservation of threatened wildlife[33]. There is an urgent need for standardized and quantitative large-scale monitoring of a variety of species and protected areas to detect and respond to changes in wildlife population sizes and thereby inform conservation management policy[34–36]. However, efforts to monitor terrestrial mammals with techniques such as camera trap grids are typically isolated and vary in methodology based on particular target species, the number and location of camera sites, length of deployment, and seasonality, making comparisons among studies difficult to achieve[37,38].

Populations of large-bodied African mammals—including those in protected areas (PAs)—have declined rapidly due to widespread habitat loss and fragmentation, over-hunting, and human-wildlife conflict[39], with megaherbivores like elephants (*Africana loxodonta*) and rhinoceros (*Diceros bicornis & Ceratotherium simium*) experiencing the greatest range contractions [40,41] and highest risk of extinction[42,43] owing to illegal trade in ivory and rhino horn. Previous studies have demonstrated that large herbivores are the key drivers of plant diversity, distribution, and cyclical succession, so monitoring of this guild is extremely important for modeling and predicting species diversity at multiple trophic levels[44–46]. Historically, large African herbivores have been counted via aerial surveys using a strip transect method, which has proven highly effective, but survey costs have become prohibitive, increasingly limiting sampling efforts.

Recently, ‘camera traps’ (CTs) have emerged as a popular tool for the systematic collection of spatial and temporal information on wildlife community traits and dynamics[12,37,47,48]. CTs are minimally invasive and inexpensive while producing massive libraries of data, which has led to a proliferation of recent projects[12,33,35,49]. Moreover, CTs collect information on entire ecological communities, though many studies focus on a single species, leaving massive troves of ‘by-catch’ images that can be utilized to study other mammal species or to evaluate interactions and predation at the population, community, or even landscape level. While these have produced valuable estimates of species richness[50,51], density[52], occupancy[53], and activity budgets[54], their power to accurately estimate species abundance and density remains a topic of debate[55,56].

Both aerial surveys and CT grids suffer from the bias of imperfect detection. Visibility bias is introduced to aerial censuses due to difficulties in spotting and counting individual animals under a variety of circumstances[57]. Vegetation density, body size, herd size/cohesion, coat color, diel activity patterns, and operational factors such as flight speed and height all affect whether an animal is observed and counted[58,59]. It has been estimated that an aerial census of wild ungulates may miss 12–77% of individuals within populations[60], depending on census method[60–62], observer effects[61,63,64], environmental variables[63,65–68], and species-specific characteristics[65,66,69]. Nevertheless, aerial surveys are still considered to be the gold standard for estimating animal abundances in African PAs.

CTs also exhibit imperfect detection, though largely as a result of animal behavior rather than environmental conditions[70]. Species and individual animals within species respond differently to the presence of stationary CTs[71,72]. Some individuals approach to investigate while others avoid the scent of humans and the noise/light emitted from the CT itself[73,74]. Due to 'trap-shyness', CTs may fail to detect individuals within detection zones[70]. Small-bodied and fast-moving species are less likely to trigger CTs' motion and heat sensors than a slow-moving, large-bodied animal[75–77]. However, CTs are considered far more effective than aerial surveys at collecting data on rare and cryptic species, particularly carnivores, which are difficult to detect from overhead and reclusive in the presence of humans. On balance, CTs yield data on more species within communities, cost less to deploy and maintain, and provide details than cannot be detected by observers in aircraft, all while costing significantly less than a single annual aerial census.

Relative Abundance Indices (RAIs) have been suggested to provide a useful tool to assess the status of focal wildlife communities[76,78–80]. even where individuals are unmarked. However, to our knowledge, no attempt has ever been made to systematically validate the population estimates of RAIs from CTs against RAIs from aerial surveys. In this paper, we test the general utility of RAIs in estimating the population sizes of 24 herbivore species across five South African nature reserves and analyze a series of factors that might be expected to cause CT grids to either over- or under-estimate population sizes relative to aerial surveys. We use data collected by the Snapshot Safari program to compare RAIs calculated from CT images at South African PAs of varying sizes, management types, and wildlife assemblages against RAIs from aerial surveys that were conducted during the same period.

Reserves

Reserves selected for this study include three in the northeast portion of South Africa in the Savanna biome (the Associated Private Nature Reserves, Madikwe Game Reserve, and Pilanesberg National Park) and two in the Nama Karoo biome on the Cape (Karoo National Park and Mountain Zebra National Park). Each participating PA in the Snapshot Safari network is represented by a three-character code throughout classification, reporting, and analyses (see Table 1.1), so we will use these codes going forward. Figure 1.1 shows where the sites are located in South Africa, along with placement of the CT grids within each. We selected these reserves to include replicates for species found within each biome while investigating the effects that habitat has on visibility for both CTs and aerial surveys. All five reserves are fenced along the outermost boundary to prevent human-wildlife conflict, which is a prerequisite required by federal law for reintroducing lions, elephants, and other large mammals to areas of previous extirpation.

Table 2.1. Descriptive stats for the five Snapshot Safari reserves selected for Relative Abundance analyses

Protected Area	Code	Size (ha)	#CTs	Coverage	Biome	Province
Assoc. Private Nature Reserves	APN	146,856	55	18.73%	Savanna/Grassland	Limpopo
Karoo National Park	KAR	75,000	20	13.33%	Nama Karoo	Western Cape
Madikwe Game Reserve	MAD	75,000	40	26.67%	Savanna	NorthWest
Mountain Zebra National Park	MTZ	28,000	19	33.93%	Nama Karoo/Grassland	Eastern Cape
Pilanesberg National Park	PLN	57,000	21	18.42%	Savanna/Desert	NorthWest

Associated Private Nature Reserves (APN)

The Associated Private Nature Reserves (collectively known as the APNR) are a consortium of small privately-owned nature reserves that are clustered on the western boundary of Kruger National Park. Since 1993, South African National Parks (SANParks) has pursued an expansion strategy to increase the amount of land available to protected wildlife. Over time, each of these privately held reserves has removed boundary fences with one another and Kruger NP to facilitate open migration throughout the South African PAs. This combined conservation land has been further integrated with Limpopo National Park in Mozambique and Gonarezhou National Park, Zimbabwe creating the Great Limpopo Transfrontier Conservation Area. Landowners in the APNR have agreed to collectively manage their lands for conservation and ecotourism purposes, and efforts are made amongst reserve managers to coordinate major prescriptive practices such as burning to ensure the best outcome for extant wildlife. The APNR is located in the Savanna biome and is dominated by impala (*Aepyceros melampus*), buffalo (*Syncerus caffer*), and a full suite of megaherbivores, including elephants, black and white rhinoceros, giraffes (*Giraffa g. giraffa*), and hippopotamus (*Hippopotamus amphibius*).

Karoo National Park (KAR) Karoo National Park is located in the Western Cape in the Nama Karoo biome endemic to southern Africa, dominated by grassy and succulent shrublands[81]. Relatively high rainfall produces communities dominated by grasses at the highest elevations with increasing aridity away from escarpment edges. Due to the absence of large predators and megaherbivores, tourists are allowed to bike and hike on trails throughout this PA and it is a popular mountain biking destination. Dominant herbivores are gemsbok (*Oryx gazella*), mountain zebra (*Equus zebra*), and kudu (*Tragelaphus strepsiceros*).

Madikwe Game Reserve (MAD)

Situated against the Botswanan border close to the Kalahari Desert, Madikwe Game Reserve was formed in 1991 largely because wildlife tourism was found to be the most fiscally and economically efficient form of land use given the poor conditions for farming. Translocations of the Big 5 species (buffalo, elephants, leopards (*Panthera pardus*), lions (*Panthera leo*), and rhinos) as well as other predators and megaherbivores have produced a diverse mammal assemblage that lends itself well to scientific discovery and experimentation. More than 10,000 mammals of 66 species were relocated from other national parks over the course of two decades. The most abundant species in

Madikwe are impala, elephant, plains zebra (*Equus quagga*), and blue wildebeest (*Connochaetes taurinus*)

Mountain Zebra National Park (MTZ)

Mountain Zebra National Park, located in the Eastern Cape Province of South Africa, was established to protect the threatened Cape Mountain Zebra. The reserve has been added to with various land parcels since 1996, including DeHoop Nature Reserve, which also hosts a Snapshot Safari grid. This has resulted in a park that has three separate pieces that are not contiguous. CTs were placed only in the largest section, which has roads where the others do not. The biome is characterized by dominant dwarf shrubs and grasses on the lower-lying valley bottom areas and plateaus with medium-sized shrubs along the moderate to steep mountain slopes[82]. (According to a 2002 management plan, mountain zebras have rebounded from a low of <80 individuals to ~1600, though the subspecies is still considered Endangered. MZNP has provided founders for ~30 subpopulations and is the source of 91% of the species' genetic diversity.) The park's most abundant species are mountain zebra, kudu, springbok (*Antidorcas marsupialis)*, and black wildebeest (*Connochaetes gnou*).

Pilanesberg National Park (PLN) Pilanesberg National Park has a unique history within South Africa. It was designed by landscape architects and had virtually no wildlife when the reserve was established[83]. Located near Johannesburg/Pretoria in an extinct volcanic crater that was pastoral farmland for many generations, the park was founded in the late '70s for the dual purposes of ecological restoration and economic development. Unlike in many other nature reserves, the resident indigenous community was consulted on the formation of the park and invited to participate in its generated economy and management decisions. Beginning in the early 1980s and throughout the '90s, various wildlife species acquired due to overstocking at other reserves were translocated to PLN. This resulted in issues with imbalances of wild animals and problematic behaviors among introduced animals[84], but those have since been corrected. Though it retains the name 'National', this PA is managed by the NorthWest Provincial authorities. Situated in the

Savanna biome, PLN has elephants and other megaherbivores, but the most abundant herbivore species are impala, plains zebra, and blue wildebeest.

II. METHODS

Camera Traps

The Snapshot Safari (hereafter Snapshot) CT deployment design, adopted by more than 45 protected areas in six countries, consists of regular grids of 20-250 camera traps spaced 2.236 km apart to create cells of 5 km^2. Grid coverage, wildlife assemblages, and habitats differ, but each research team has deployed CTs in the same manner to facilitate cross-PA evaluations of wildlife and conservation outcomes. CTs are secured with steel cases and attached to trees at ~50 cm height to detect medium- to large-bodied mammals. CTs are not intentionally positioned at waterholes or other landscape features, but face a feature or game trail when possible. When passive infrared sensors are triggered by motion or heat, each CT is programmed to take a series of three images within ten seconds of each other (a 'capture event') with a one-minute rest between captures during the day[12]. Overnight, cameras take only one picture to save battery power and the rest period remains one minute. Memory cards and rechargeable batteries are changed approximately every ten weeks. Most grids in South Africa have operated continuously since 2017 or 2018 and are intended to run for a decade or longer. Metadata on camera placements and habitat characteristics are also collected in a standardized manner at deployment, including elevation, categorical shade values, and the distance to the nearest ten trees.

As a result of this deployment methodology, Snapshot CTs generate large volumes of photographs, which makes species classifications highly time-consuming. To facilitate efficient image processing, we combine citizen science efforts with advanced machine learning techniques.[11] Snapshot partners with the citizen science platform Zooniverse, where volunteers identify species and annotate other data such as the number of individuals, behaviors, and demographics visible in each capture. More than 200,000 volunteers worldwide have classified over 12 million photographs since the relaunch of

Snapshot as a network in February 2018. These responses exhibit 97% accuracy, confirming the reliability of citizen science in rapidly processing large volumes of data[12].

The Snapshot network also incorporates machine learning (ML) algorithms prior to uploading data to Zooniverse to decrease the number of citizen scientists required to view each capture event[11,85]. Two image classifiers (convolutional neural networks) are employed; one to identify empty images and one to predict the species, counts, and behaviours in images containing wildlife. The algorithms' predictions and confidence levels are uploaded to Zooniverse with the image manifest and used to dynamically determine the level of agreement and number of volunteers required to confirm the algorithms' label. The millions of images generated annually by the Serengeti grid have been utilized as training data for many deep learning algorithms developed to identify African mammal species automatically[11,20,21].

Aerial Surveys

Aerial surveys in South Africa are conducted during the dry season (May – September), typically in September when obstruction from vegetation is at its lowest point. Due to the low degree of detectability from the air for carnivores, observers focus on large herbivores and record predator numbers opportunistically, if at all. The entire survey site is flown once over the course of 1-4 days depending on the size of the reserve. The aerial survey method is similar at all five PAs, with slight differences among them. For all five reserves, helicopters using roughly the same method as described below were used for surveys.

At the APNR, aerial censuses were conducted via Bell Jet Ranger helicopter with a crew consisting of a pilot, ecologist, and two observers. Helicopters flew at 40-60 knots at a height of 120 feet in transects ~400 m wide. The craft hovers over large herds of animals to give observers more time to accurately count large groups of animals. APNR counts are geo-tagged to provide detail on species/herd distributions. The aerial results for the other four reserves are aggregates of the total count of each species without geo-tagging.

At Madikwe Game Reserve (MAD), the entire reserve is censused on three consecutive days three different times over the course of a survey year for a total of nine passes. The census data was recorded as both an average and the total observed—for this study, we use the averaged numbers. Due to this more intensive procedure, MAD aerial surveys are conducted biennially while the other four PAs returned annual counts. We therefore include data from 2018 and 2019 for four sites and 2018 only for MAD.

Statistical Evaluations

For these analyses, all herbivores were evaluated to assess the efficacy of CTs in picking up animals detected by aerial censuses in different habitats. Table 1.2 documents the herbivores expected to occur at each of the five reserves, which differ to varying degrees, but especially between the Savanna and Nama Karoo sites. Species in which no animals were sighted by one or the other method were removed from subsequent evaluations. Rhinoceros were excluded at the request of reserve managers due to their critically endangered conservation status and vulnerability to illegal offtake.

RAIs from CT grids were calculated by compiling the number of 'captures', e.g. instances when a particular species triggered a camera's motion sensor, as well as the total number of individuals within each capture. Independent capture events were derived by a 10-minute lag between images of the same species at the same camera to prevent oversampling. The independent records were used to calculate the number of sightings based on search effort (numbers of cameras x number of operational days). The relationship between RAIs produced from each survey method was analyzed using log–log regression.

All statistical evaluations were conducted in R v. 4.2.2 (R Core Team, 2021). Results were considered significant at 0.05. Maps and GIS representations were produced using ArcGIS software.

Table 2.2. Herbivore assemblages at each of the five focal reserves with traits that may influence how well they are documented by either CTs or aerial surveys. An ‘x’ below the reserve abbreviation indicates an extant herbivore population. The listed body mass is averaged between males and females.

Herbivore Species	Scientific Name	Weight (kg)	Group Size	Diet	APN	KAR	MAD	MTZ	PLN
Blesbok	*Damaliscus pygargus phillipsi*	62	Gregarious	Variable Grazer				x	
Buffalo	*Syncerus caffer*	600	Mega-groups	Variable Grazer	x		x	x	x
Bushbuck	*Tragelaphus scriptus*	38	Solitary/pairs	Browser	x				
Duiker (Common)	*Sylvicapra grimmia*	13	Solitary/Pairs	Browser		x			
Eland	*Taurotragus oryx*	600	Gregarious	Browser-Grazer-Intermediate		x	x	x	x
Elephant	*Loxodonta africana*	4275	Gregarious	Browser-Grazer-Intermediate	x		x		x
Gemsbok/Oryx	*Oryx gazella*	225	Gregarious	Variable Grazer		x	x	x	
Giraffe	*Giraffa g. giraffa*	899	Gregarious	Browser	x		x		x
Grey Rhebok	*Pelea capreolus*	19	Family	Browser				x	
Hartebeest	*Alcelaphus buselaphus*	135	Gregarious	Variable Grazer		x	x	x	x
Hippopotamus	*Hippopotamus amphibius*	1417	Gregarious	Variable Grazer	x		x		x
Impala	*Aepyceros melampus*	51	Gregarious	Browser-Grazer-Intermediate	x		x		x
Kudu	*Tragelaphus strepsiceros*	215	Family	Generalist-Herbivore	x	x	x	x	x
Nyala	*Tragelaphus angasii*	85	Family	Generalist-Herbivore	x				
Reedbuck (Mountain)	*Redunca fulvorufula*	30	Family	Obligate Grazer		x		x	x
Springbok	*Antidorcas marsupialis*	36	Mega-groups	Browser-Grazer-Intermediate		x		x	x
Steenbok	*Raphicerus campestris*	12	Solitary/pairs	Browser-Grazer-Intermediate		x	x	x	
Tsessebe	*Damaliscus lunatus*	136	Mega-groups	Obligate Grazer			x		x
Warthog	*Phacochoerus aethiopicus*	83	Gregarious	Omnivore	x		x	x	x
Waterbuck	*Kobus ellipsiprymnus*	218	Family	Variable Grazer	x				x
Wildebeest (Black)	*Connochaetes gnou*	146	Gregarious	Variable Grazer				x	
Wildebeest (Blue)	*Connochaetes taurinus*	204	Mega-groups	Variable Grazer	x		x		x
Zebra (Mountain)	*Equus zebra*	255	Family	Variable Grazer		x		x	
Zebra (Plains)	*Equus quagga*	273	Family	Obligate Grazer	x	x	x		x

III. RESULTS

We first compared population estimates from camera trap surveys with totals from the aerial surveys, using data weighted by the number of individuals captured in each photo vs. unweighted estimates that only considered the number of capture events for each species. Across all species in each of the five reserves, *weighted* estimates (referred to henceforth as RAIs) were more closely correlated with the aerial surveys (i.e., RAIs always produced stronger correlations with species abundance in the aerial surveys) than were the unweighted estimates, as was previously reported for the Snapshot Serengeti grid[76]. Similarly, RAIs from the dry season, May-Sept., yielded the highest cross-species correlations with the aerial survey counts. Extending the length of the survey period to a full year did not improve the correlations; we therefore restricted our analyses to RAIs collected during the dry season each year.

Although RAIs and aerial surveys provide broadly similar results *across* species (i.e., both agree on which species are the rarest or most common), within-species estimates diverged to varying degrees for each species. To provide a consistent comparison between the two methods, we relied on the ratio of the RAI estimate for each species divided by the aerial count for that same species each year. By this measure, underestimates are indicated by values <1 while overestimates are >1. We refer to this ratio as the "relative accuracy" of the RAIs, and, as seen in the following figures, these generally underestimated the population totals compared to the aerial surveys. Looking across all the data for all species that were counted in both 2018 and 2019, there were 43 possible comparisons (on species for which >50 individuals were seen from the air) to evaluate if the RAIs agreed with the aerial surveys as to whether population size rose or dropped from one year to the next. The two measures agreed on the direction of change only 48.8% of the time. Furthermore, there was no effect of the magnitude of the change in the successive aerial counts on whether the RAIs correctly predicted the direction of change.

Because of the striking contrasts in vegetative cover and hence the cameras' typical field of view between the five reserves, we first examined the extent to which tree density affected the relative accuracy of the RAIs for each species. Figure 2.2 shows the relationship between the average distance from the cameras to the nearest trees and the relative accuracy of the RAIs for each species that was measured in at least two different reserves. Though average tree distance ranged from nearly 100 m (in MTZ) to only 5 m (in MAD), the accuracy of the RAIs only improved with increasing visibility in 8 of 17 species. In fact, of the eight positive trends, seven were driven by the data from MTZ; excluding that site, the RAIs generally underestimated the aerial survey numbers to a greater extent in more open habitats. Figure 2.2 also shows that the accuracy of the RAIs within each reserve was only closely similar from one year to the next in two reserves for impala and blue wildebeest and a single reserve apiece for kudu, giraffe, warthog, and eland. Most other estimates differed substantially in successive years; thus, we consider each annual survey separately for each reserve in all further analyses.

Figure 2.3 compares the extent to which each species was under- or over-estimated in each of the four reserves where data were available for both 2018 and 2019. In all four reserves, individual species were over- or underestimated to roughly the same extent each year (as indicated by the regression lines in each comparison). For example, kudu were overestimated to the greatest extent in both surveys in MTZ, as were warthog in PLN, whereas hartebeest were strikingly underestimated both years in KAR, as were mountain reedbuck in PLN. Note again how some species estimates varied from one year to the next (e.g., buffalo in the APN and PLN) and that the relative accuracy for individual species varied strikingly across reserves: kudu was the only species found in all four of these reserves, and whereas the RAIs overestimated kudu numbers in MTZ, the RAIs greatly underestimated kudu numbers in PLN.

Given that the relative accuracy of the RAIs varied to roughly the same extent from one year to the next across species, what are the factors that might improve or diminish the detection rate of any particular species within the camera grid? While larger animals are readily detected from a low-flying aircraft, smaller species may remain unseen in tall grass or in woody vegetation. Conversely large animals move over larger areas and therefore may be more likely to trigger a camera. However, bodyweight showed no obvious effect on the relative accuracy of the RAIs in most of the nine surveys (Figure 2.4).

Species abundance might also be expected to affect the accuracy of the RAIs. On the one hand, more abundant species might be expected to trigger more camera photos as there are simply more agents that might pass close to a camera. On the other hand, more abundant species also live in larger herds, and cameras may only detect a subset of any given aggregation. However, there was again no clear relationship between the accuracy of the RAIs compared to the aerial counts in most of the surveys (Figure 2.5).

Finally, RAIs depend on the extent to which animals are evenly distributed across the entire camera grid. If individuals are highly clumped, they may only be captured at a single trap, whereas more evenly distributed species can potentially be captured at every camera in the grid. As a simple measure of “evenness” we calculated the variance in the proportion of camera trap counts for each species collected at each site. (Note: GIS representations of how species arrayed themselves across the CT grid in each landscape are included in the Supplementary Materials.) As expected, species whose distributions were most clumped were most severely underestimated (Figure 2.6). However, though this was the case in 8 of the 9 surveys, the trends were generally quite weak, suggesting that additional factors may play a bigger role on the relative accuracy of RAIs than our simple measure of cross-site variance.

IV. DISCUSSION

Snapshot Safari is unique in the depth and breadth of our data collection. With >1500 stationary CTs operating continuously in 45 PAs, ~2 million images are generated annually. The camera grids capture ~75-100 mammal species in most PAs, providing information on demographics (e.g., age/sex distributions[19], behaviors (e.g., resting, standing, moving, eating)[35], and grouping patterns[14,86]. We focused here on RAIs because they are so simple to calculate and the have the potential for informing PA mangers about their success at conserving African wildlife. We hoped to find consistencies that allowed for correction factors or other statistical approaches that could provide low-cost alternatives to aerial surveys for estimating population sizes and population changes, but our results revealed high variability across reserves, species, and years.

RAIs and aerial surveys are both imperfect, but accepting the flight data as our gold standard, the correlation between the two measures is erratic from reserve to reserve and only slightly affected by species characteristics (bodyweight, abundance, and spatial distribution). Looking at the one species measured in all five reserves, kudu were overcounted both years in MTZ, but undercounted everywhere else, perhaps suggesting that kudu only happened to select foraging patches inside the MTZ camera grid or kudu were exceptionally visible in this most open of the five reserves. In contrast RAIs of buffalo and plains zebra in APN and buffalo in PLN varied by over an order of magnitude from one year to the next. Did key resources shift from one part of the reserve to another? Or are RAI estimates so inherently noisy as to be useless for monitoring populations of these species?

The stochastic variability across species and years might be reduced by ensuring that the entirety of each reserve is covered by a camera grid rather than a portion of it. But if this succeeded, larger grids would be considerably more costly, and many PAs lack the funding to make an investment in a CT grid of that size, thus reducing any financial advantages over aerial surveys. However, our nine annual surveys were only conducted over two years, and the continued accumulation of both types of data over multiple years might allow for the development of statistical models that could accurately detect population density and trends despite the variability that we encountered in this paper.

Increasingly sophisticated machine-learning models may also play an important role in future efforts to track and monitor wildlife populations. Training algorithms to identify individuals within animal populations might eventually allow for use of spatially capture-recapture (SCR) models on certain species (especially those with distinctive pelage like zebra, giraffes, and leopards, while elephants can be recognized by their ear patterns and notches and lions by their whisker spots and scars). ML algorithms require large amounts of training data, so the CT data created and curated by Snapshot will be highly beneficial for developers and ecologists seeking to use individual recognition in their systems. If such algorithms are successful for a particular species, they could be used to retroactively track population sizes and trends from earlier surveys. Future work will involve testing a variety of models including SCR on Snapshot data to evaluate performance on unmarked animals.

FIGURES

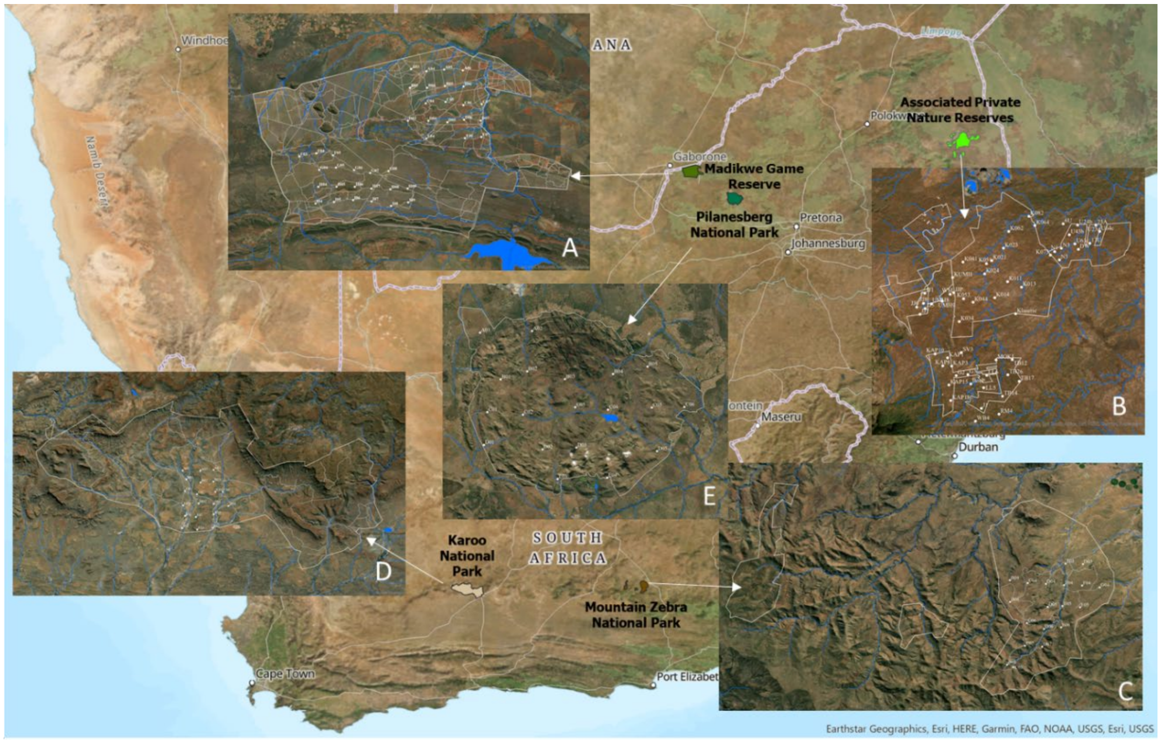

Figure 2.1. Map of South Africa with the five focal reserves outlined and insets showing the distribution of cameras at each site. Clockwise from top: A) Madikwe Game Reserve (MAD), B) Associated Private Nature Reserves (APN), C) Mountain Zebra National Park (MTZ), D) Karoo National Park (KAR), and E) Pilanesberg National Park (PLN).

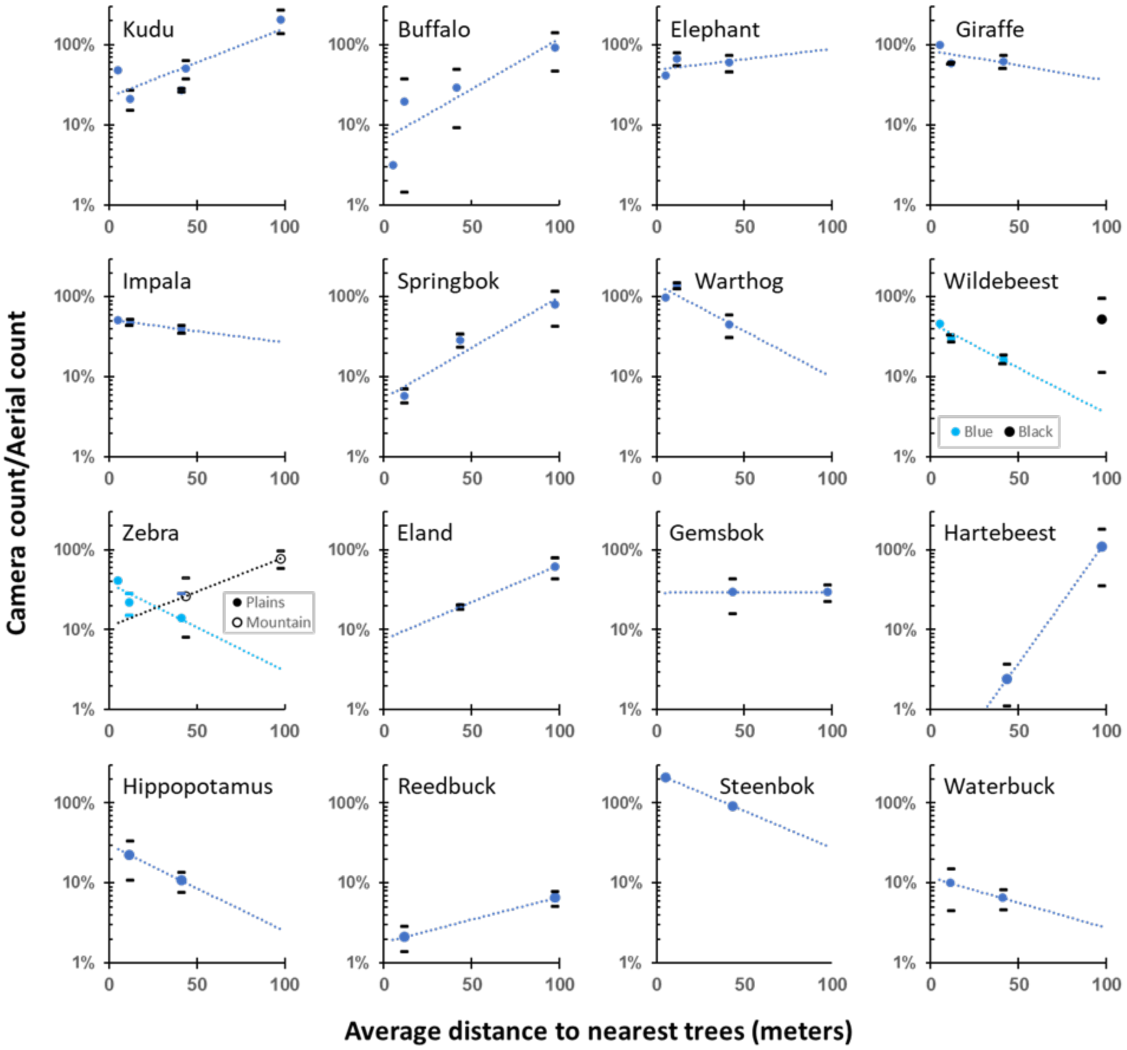

Figure 2.2. Relative accuracy of the RAIs for each species in each reserve plotted as a function of the average distance from the camera traps to the nearest trees. Dashes indicate the relative accuracy of estimates measured in 2018 and 2019; single measurements lack dashes. Species are arranged in descending order of the number of reserves in which they were measured (from five reserves for kudu to two for mountain zebra through waterbuck); black wildebeest were only present in a single reserve but are included for comparison with blue wildebeest.

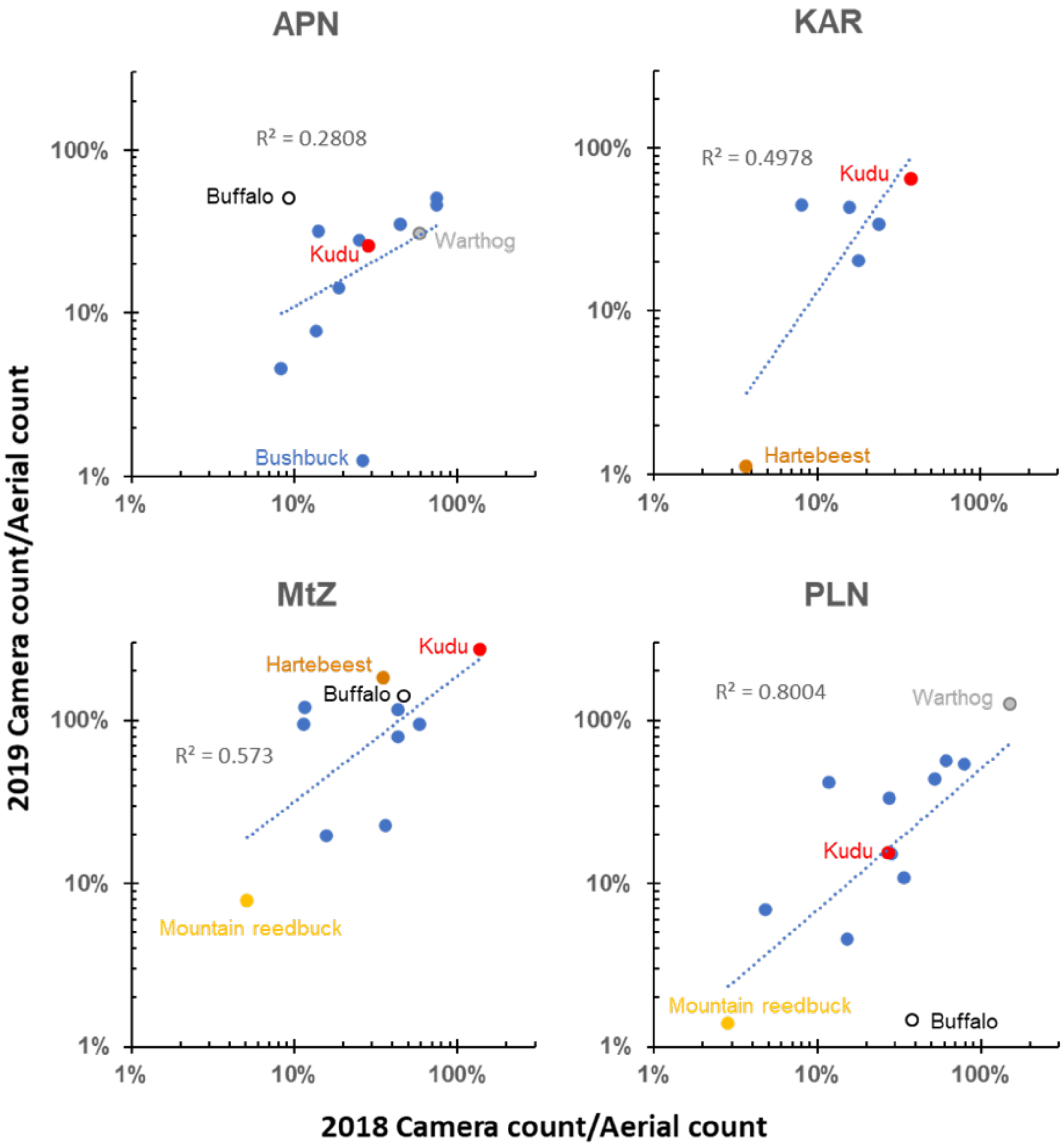

Figure 2.3. Comparison of the relative accuracy of camera trap surveys for each species during successive dry seasons (MAD not included as it only had one dry season with overlap from both survey methods). Notable species are labeled (see text). Data for each survey are restricted to species where at least 50 individuals were counted from the air and at least 1 individual was photographed by a camera-trap.

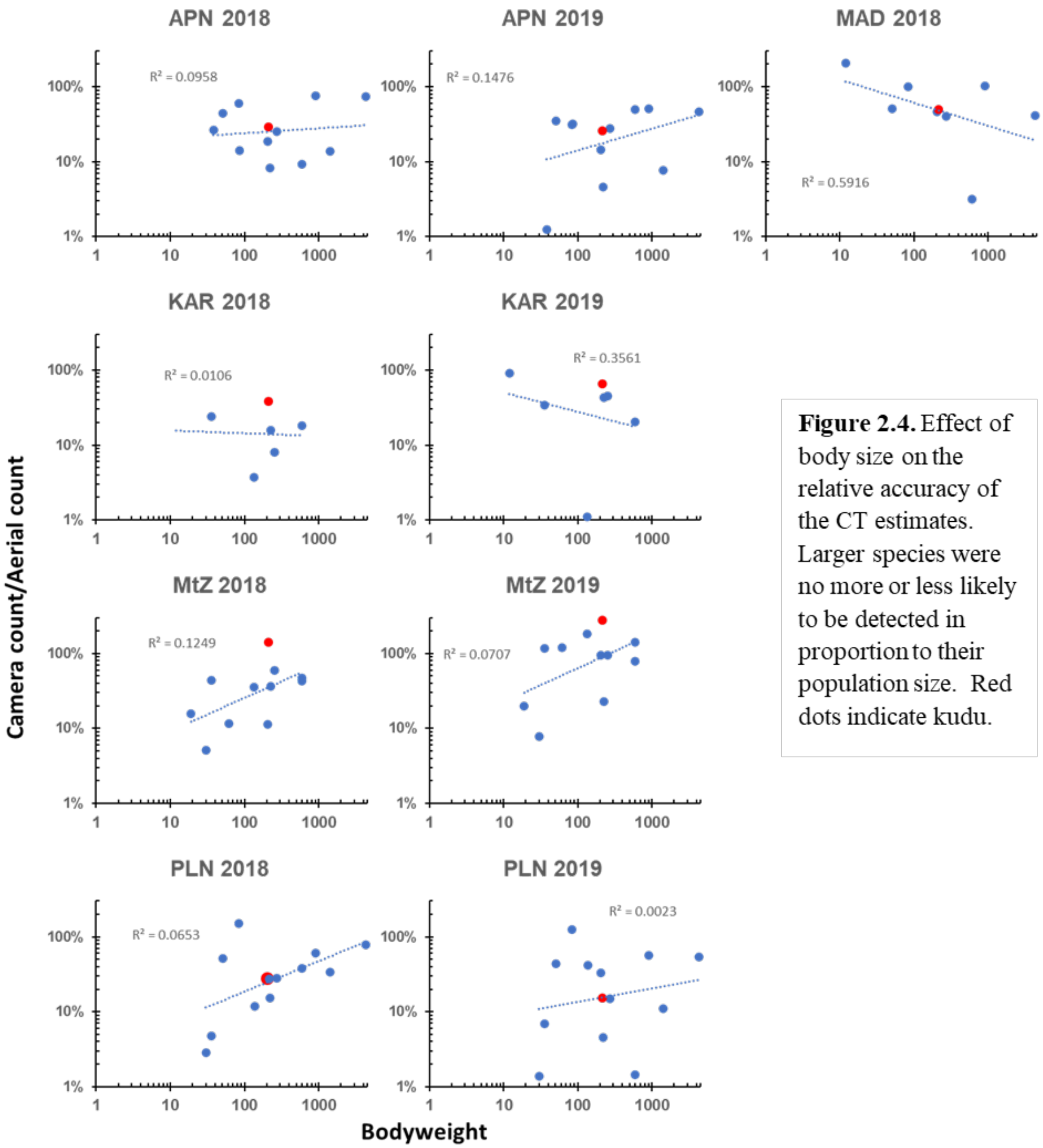

Figure 2.4. Effect of body size on the relative accuracy of the CT estimates. Larger species were no more or less likely to be detected in proportion to their population size. Red dots indicate kudu.

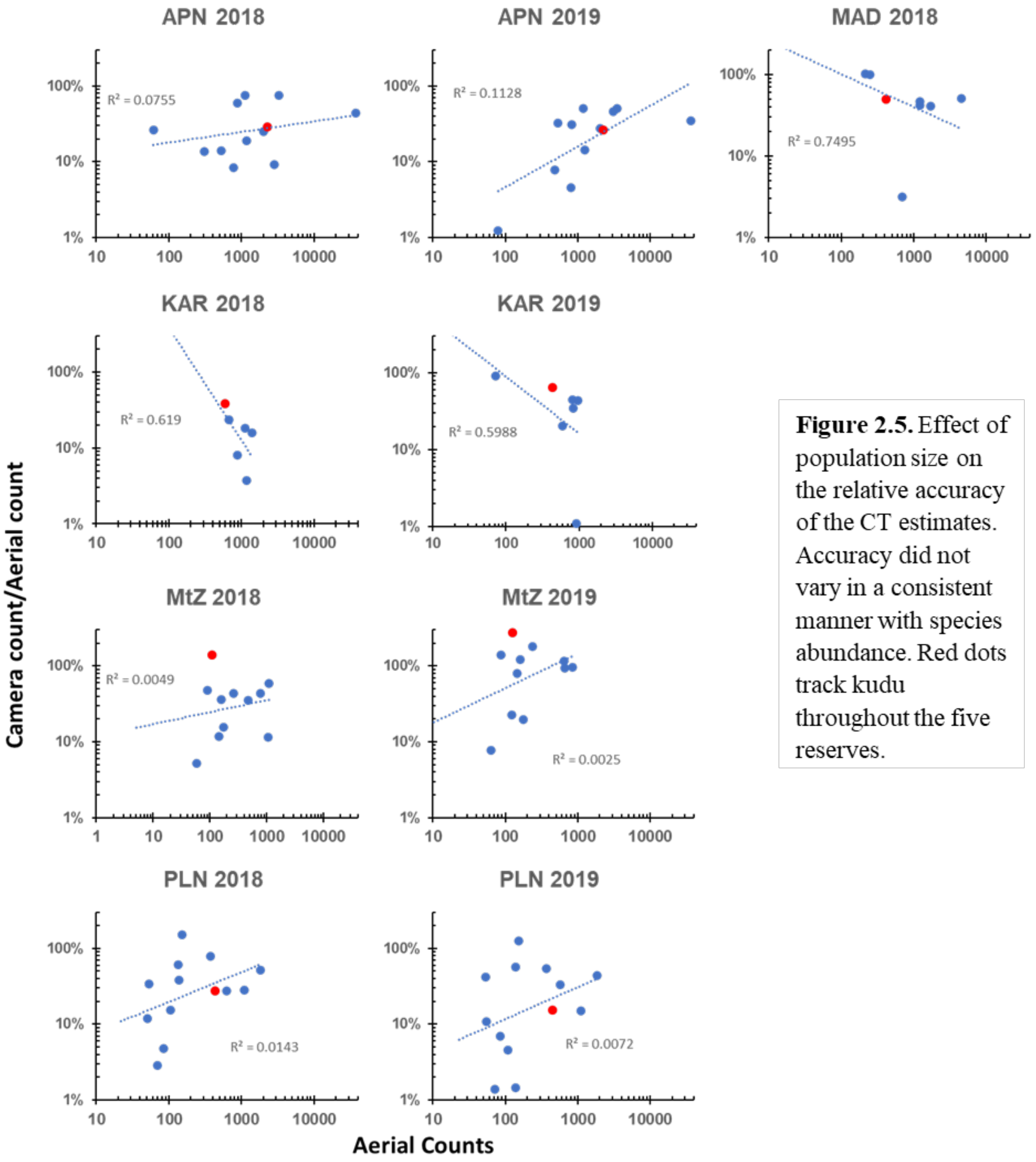

Figure 2.5. Effect of population size on the relative accuracy of the CT estimates. Accuracy did not vary in a consistent manner with species abundance. Red dots track kudu throughout the five reserves.

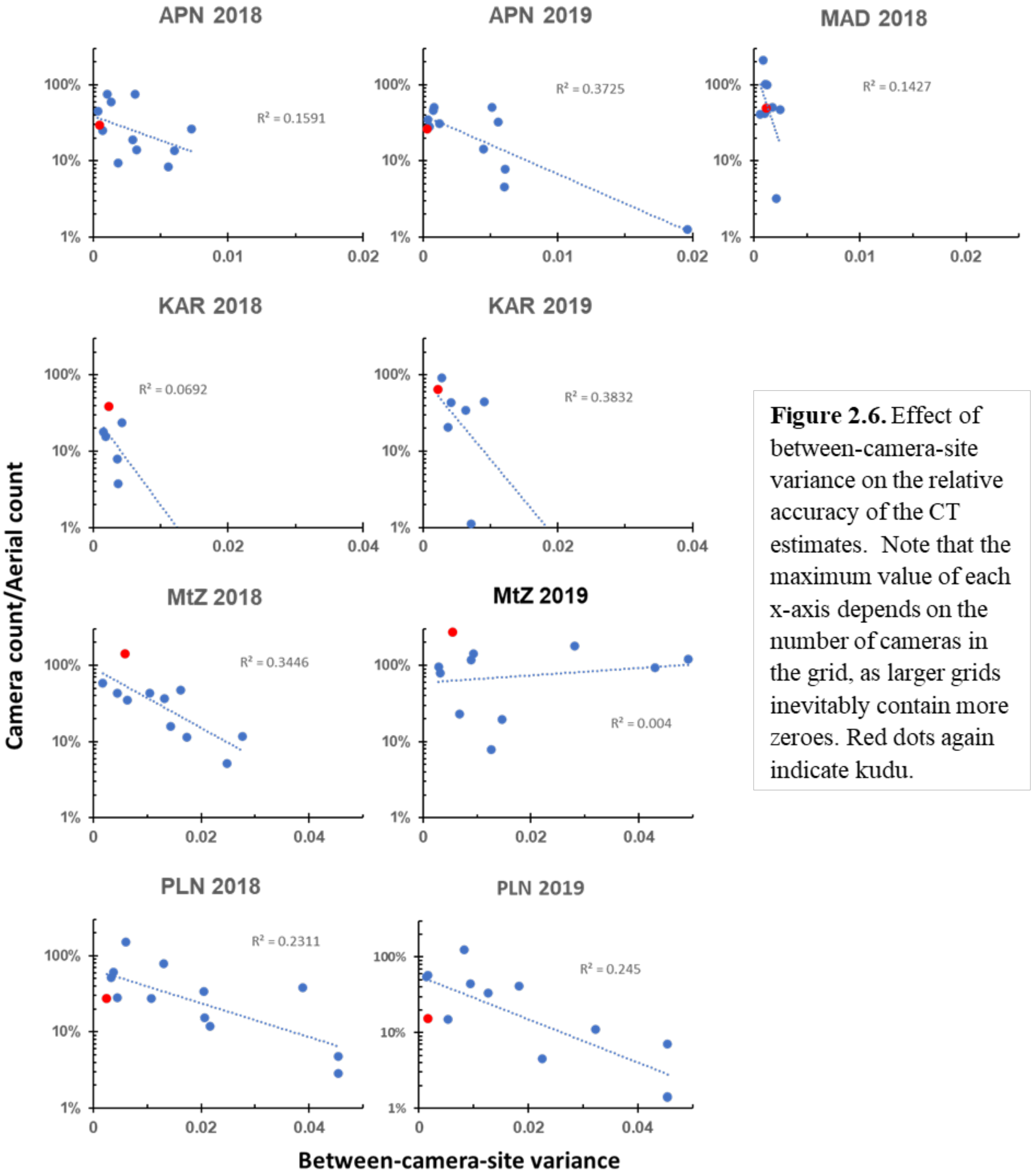

Figure 2.6. Effect of between-camera-site variance on the relative accuracy of the CT estimates. Note that the maximum value of each x-axis depends on the number of cameras in the grid, as larger grids inevitably contain more zeroes. Red dots again indicate kudu.

Chapter 3

The Elephant Problem, Revisited

with Mike J.S. Peel and Craig Packer

ABSTRACT

Conservation of elephants can be challenging, particularly if conflict with humans cannot be avoided. In South Africa, where elephant populations continue to expand, more space is often needed to meet their resource requirements. As part of an expansion strategy developed by Kruger National Park to provide more territories for wildlife, several privately owned protected areas collectively known as the Associated Private Nature Reserves have removed boundary fences that once excluded wildlife from KNP. The sequential removal of fences provides a unique natural experiment in which elephants have reoccupied tracts of land along a temporal gradient. Here, we present results from several decades of vegetation surveys combined with 14 years of aerial counts to investigate the extent to which elephants have altered four neighboring conservancies in the APNR after the removal of perimeter fencing allowed the return of elephant herds from KNP. Our analyses suggest that elephants have had little, if any, effect on three of the most abundant herbivores and two highly valued tree species in the APNR as they recolonized new areas of previous extirpation.

I. INTRODUCTION

Conservation of elephants (*Loxondanta africana)* in a world of shrinking resources is inherently fraught[40]. Due to their massive nutritional needs and potential for damaging human structures and crops, elephant conservation can cause conflict with local residents[87–89] and conservationists tasked with preserving overall biodiversity[90] or sustaining mature trees and woodlands[91,92]. Effective management of African protected areas requires safeguarding endangered and rare plant species as well as sustaining the charismatic wildlife that drives the ecotourism industry[93,94]. Nowhere is the ‘elephant problem'[95] more evident than in South Africa, home to a global biodiversity hotspot[96], hundreds of endemic plant species[97], and locally increasing elephant populations[98]. Because South Africa's economy is heavily dependent on ecotourism revenue, conservation management decisions are often based on aesthetics or tourists' perceived preferences rather than the maintenance of biodiversity or overall conservation effect[99]. Elephant translocations were common in the post-apartheid era (1990s) because a spate of new nature reserves were established with the intent of profiting from international ecotourism[98,100]. Many reserves chose to introduce elephants without thorough consideration of the ecological consequences of reintroducing megaherbivores (>1000 kg) into confined areas, nor the practicalities of ongoing intensive management required to maintain such populations within the boundaries of a reserve[101,102]. When elephants predictably deplete the savanna woodland and cause mature tree mortality, calls to cull them ensue[92,103]. Controversy over elephant carrying capacities and effects on mature trees (>5 m in height) within fenced reserves in South Africa has led some to view current elephant populations as untenable[104]. Others take the opposite view in light of the positive effects elephants have on biodiversity at other trophic levels, particularly for smaller mammals and reptiles[105,106]. The array of management strategies undertaken in South Africa provides the opportunity to evaluate the effects of elephants on multiple trophic levels under a variety of environmental conditions.

The artificial provision of surface water to supplement wildlife populations has been a common management intervention in South Africa since the 1930s, including in its oldest wildlife reserve, Kruger National Park (KNP). Protected areas (PAs) in South Africa are required to have perimeter fencing to prevent human-wildlife conflict, but this eliminates the ability of wildlife to use migratory pathways that existed prior to human land-use transformation. To compensate, over 365 boreholes were dug in KNP between the 1930s-1980s, and more than 50 new dams were erected on natural water sources[107]. This was done in tandem with the adjacent nature reserves collectively known as the Associated Private Nature Reserves (APNR), where dozens more artificial water sources were created (see Figure 3.1). The program was intended to minimize the effects of seasonal variability in water to maximize potential game viewing for visitors[108]. But in the 1980s, the homogenizing effects of densely spaced waterholes became evident as forage composition changed[109] and water-dependent species flourished while rare antelope species declined[110]. Consequently, KNP officials closed more than half of the artificial waterholes in the park between 1994-1999[111], but artificial waterholes in the APNR remain open and abundant. Since culling ceased in 1994, the elephant population in KNP/APNR has more than doubled (~17,000 individuals as of 2015)[112]. While elephants remain close to water sources during the dry season, resulting in greater damage to the immediate area[113], water provisioning also allows foraging elephants to extend their normal range and impact additional regions of a PA[114].

Landscape-Level Effects

Heterogeneity/species richness

Savanna elephants are well-known ecosystem engineers[115], a term given to animals that physically modify their habitats[116]. Elephants alter the structure of the savanna via their foraging habits (toppling or removing parts of mature trees), migration patterns, and interactions with other organisms in their environment[117,118]. Elephants are the primary driver of treefall in KNP, particularly trees in the 5-8 meter height class[119]. The presence of elephants has been negatively correlated with a reduction in woody cover, leading to concerns about a corresponding reduction of valuable tree species and a concomitant reduction in biodiversity as woody cover is lost[90,120]. Degradation of grasslands, wetlands, and riparian areas has forced elephants to subsist on woody vegetation for longer periods of the year, prolonging their impact on certain species and potentially driving them toward extirpation[121].

Increasingly, however, the keystone role of elephants in maintaining vegetational heterogeneity in savannas has been positively acknowledged[122–124], particularly for small vertebrate species[125,126] and in densely wooded landscapes[127]. South Africa is contending with woody encroachment in many of its managed landscapes, which can modify the herbivore assemblage, decrease grass biomass, and lower fire frequency[128]. Elephants reduce encroachment by clearing woody cover, producing litter, and forming new paths through thickets[94].

Limitations of movement

When unrestrained by human intervention, individual elephants can range over 10,000 km^2 and exploit a wide variety of habitats while exhibiting high fidelity to previously successful resource sites[129]. As human populations continue to expand, elephants are forced into smaller territories and, often, fenced within the PAs to prevent dispersal. The electric fencing employed by most reserves elicits a high degree of avoidance behavior, creating an edge effect that further increases intensity of use around waterholes and toward the center of the reserve[130].

Demographics also influence movement patterns—bulls range farther from water sources while maternal herds with calves demonstrate high dependence on water availability with a preference for riverine habitat during the dry season[114]. Under normal ranging conditions, elephant foraging effects are varied across the landscape, resulting in 'piospheres' or gradients of elephant impacts that are highest near water sources and recede with distance[131]. If sufficient artificial waterholes are provided, these landscape-level effects may cause large overlapping zones of decimated trees[132,133]. Because fenced elephant populations grow quickly, this can lead to untenable situations where recruitment of tree populations is continually limited[134]. It has been hypothesized that due to the imbalance of water provisioning, higher numbers of elephants are occupying habitat in the APNR than in KNP during the dry season, with resultant homogenization of forage and losses of diversity at lower trophic levels, but this has not yet been supported by direct evidence.

Synergistic effects with fire on establishment and recruitment

Rain, soil nutrients, fire, and herbivory are the four primary drivers of vegetational heterogeneity in savanna ecosystems[135], but their relative influences are often difficult to parse given their interactive nature. Fire and elephant herbivory have most often been studied to assess their impacts on woody cover[136–140], and research in the Kruger has demonstrated that the synergistic effects of elephants and fire are most likely to cause loss of biodiversity at multiple trophic levels[126,141,142].

The ability of seedlings to outlive the ‘fire trap’, e.g. grow tall enough to escape fire, is key to the persistence of savanna woody species[143]. Thus browsing by smaller herbivores also plays a major role in limiting recruitment following elephant damage[139,144], and these combined effects may explain the drive towards extirpation of certain species[145]. Due to the stochasticity inherent in savanna systems, impacts of elephants and other browsers are highly site-specific and require local and targeted evaluations[146] and management at appropriate spatial scales[147].

Behavioral Interactions/Indirect Effects

Elephants primarily interact with other herbivores through indirect effects caused by landscape modification and occasionally by direct competition over browse resources. However, the complexity of African savanna systems can produce confusing and conflicting results. An experimental study to quantify the effects of elephants on browse availability for their primary competitor, black rhinoceros (*Diceros bicornis*), found both facilitation and exclusion[148]. Black rhinos initially benefit from the paths that elephants clear, allowing passage through otherwise impenetrable thicket, but elephant resource utilization eventually leads to decreased browsing opportunities. We hypothesize that a similarly contradictory dynamic may also affect elephant interactions with giraffe (*Giraffa camelopardalis)* and ungulate mesobrowsers like greater kudu (*Tragelaphus strepsiceros*) and impala (*Aepyceros melampus*).

At another privately managed reserve bordering KNP that allowed elephant recolonization through fence removal, researchers found that higher elephant densities alter the structure of herbivore communities over time, favoring higher abundances of grazers and decreasing numbers of browsers[120]. Other studies have noted that elephants enhance browse heterogeneity by maintaining trees and shrubs below a certain height, e.g., ‘browse lawns’[149] and that trees heavily browsed by elephants regrow shoots of higher nutritional quality, which facilitates smaller browsers like duiker (*Sylvicapra grimmia*) and steenbok (*Raphicerus campestris*)[106]. Both biomass and species richness for understory plants increase beneath elephant-damaged trees, suggesting that elephants exert positive indirect effects on a variety of plants and animals[150].

Elephants can also alter the landscape for other herbivores by changing where predators encounter prey. One study found that predators had greater success killing small prey in fragmented thickets that had been browsed by elephants[151], and another documented more lion kill sites in elephant-impacted areas[152]. Both studies hypothesized that these patterns resulted from enhanced predator access into woody areas and more suitable ambush sites. Accumulating evidence supports the possibility that megaherbivores like elephants (immune from predation due to their massive size as adults) can create dynamic 'landscapes of fear'[153] for prey species[154,155].

Here, we present results from several decades of vegetation surveys combined with 14 years of aerial counts to investigate the extent to which elephants have altered four neighboring conservancies in the APNR after the removal of perimeter fencing allowed the return of elephant herds from KNP.

II. METHODS

Study System

The APNR is a consortium of private landowners whose properties (Balule Nature Reserve, Klaserie Private Nature Reserve, Thornybush Nature Reserve, and Umbabat Private Nature Reserve) are contiguous with the western boundary of KNP (see Figure 3.1). These small, fenced reserves presented a particular management problem after Klaserie and Umbabat Nature Reserves removed boundary fencing with KNP in 1993, Balule Nature Reserve in 2003, and Thornybush in 2016. Neighboring Kapama Game Reserve still maintains an intact perimeter fence, providing our study a control site containing a small herd of only 50 elephants. All five conservancies are located in the eastern Lowveld.

Aerial Surveys

Aerial surveys of medium- to large-bodied herbivores conducted during the dry season (May – September), typically in September when obstruction from vegetation is at its lowest point. The entire survey site is flown once over the course of 1-4 days depending on the size of the reserve. Censuses were conducted via Bell Jet Ranger helicopter with a crew consisting of a pilot, ecologist, and two observers. Helicopters flew at 40-60 knots at a height of 120 feet in transects 200 m wide on either side of the craft.

Vegetation Surveys

The woody layer within the APNR reserves was monitored annually in November–December from 1993 to the present by the Animal Production Institute of the Agricultural Research Council (ARC-API) using a 100 × 2-m belt transect in each of ~200 permanent plots in which the number of all woody plants within a belt transect over four height classes (1: 0-1 m, 2: 1.1–2.0 m, 3: 2.1–5.0 m, 4: >5.1 m) was recorded, together with the numbers of stems per woody plant[156]. The standing crop of the herbaceous layer was recorded from 1997 onward using a disk pasture meter which measures the herbaceous standing biomass in the presence of fire, herbivory, plant senescence, and decomposition[157]. Snapshot Safari cameras were placed directly on select transects in 2017/2018 (55 total) to assess wildlife capture rates in relation to historic vegetation data; however, that data is not reported as the camera trap survey began in 2017/18 and does not overlap with the vegetation and aerial surveys relied on here.

III. RESULTS

Figure 3.2 summarizes the population trends of elephants, giraffe, impala, and kudu in the five conservancies, as measured by annual aerial surveys. Elephant abundance steadily increased (except for the small stable population of ~50 elephants in the still-fenced Kapama conservancy), with an especially striking increase in Thornybush when the boundary fence was removed in 2016.

To evaluate how dependent elephants are on rainfall in the APNR and Kapama, we looked at how their density varied across a gradient of annual precipitation (Figure 3.3). There was no significant effect of respective rainfall totals on elephant densities in the four unfenced conservancies, suggesting elephant movements are not highly dependent on natural weather patterns in this system.

We next measured how elephant density affected the abundance and density of two key tree species within this system: marula (*Sclerocarya birrea*) and knobthorn (*Senegalia nigrescens*). Each species is abundant in KNP/APNR and favored by elephants. The marula is also highly valued by humans for its medicinal properties and its fruits, which are eaten and fermented into beverages. To assess how trees are faring in the APNR post-elephant recolonization (with Kapama as the control), we analyzed each of the four height classes independently within each species and reserve (Figure 3.4). In addition to elephant density, variables with possible explanatory power include distance to closest trees, shade, precipitation, and reserve. The full statistical models suggested that of these, elephant density and precipitation might be most important, so we restricted our model to those variables for final analysis (see Tables 3.1-3.16 in Supplementary Materials). We calculated the change in density within each height class at one- and two-year intervals after exposure of observed elephant densities and created linear regression models to ascertain which variables significantly influenced the change. There was no measurable effect of elephant density for any height class of marula or knobthorn, including class 4, mature trees >5 m tall.

Turning to herbivores, we calculated the annual population densities of elephants, giraffe, impala, and kudu at each reserve using aerial survey counts for the years 2004-2018. Elephants are mixed feeders and could potentially affect both grazers and browsers, but we focus here on browsers since trees are slow-growing and less abundant than other forage resources. Giraffes are exclusively browsers and typically feed at the height of 3-5 meters while elephants may select anywhere between 0-5 meters, so it is possible there could be competition for the same woody resources[158]. Impala are medium-bodied browsers that typically browse below 1 meter in height, so high densities of impala may have a limiting effect on tree recruitment, and they likely experience minimal competition with elephants beyond temporary patch displacement. Kudu have a large overlap with impala and typically feed between 0-2 meters.

Using the same variables as the tree models, we performed linear regressions on the change in density for each herbivore species with 1- and 2-year lags to evaluate the influence of increasing elephant density. There was no measured effect on the density or the change in density for any of the three species. Although kudu abundance dropped coincident with the initial return of the elephants in Thornybush in 2016 (Figure 3.5), kudu did not show a consistent decline with increasing elephant density across all the reserves. Regression results can be found in Tables 3.17-3.22 in Supplementary Materials.

IV. DISCUSSION

Decades of research on elephants' environmental impacts provide a rich literature with sometimes contradictory findings. While the focus of many projects has been on the loss of mature trees and species richness, more recent research suggests that a more nuanced approach is prudent. Elephants facilitate grass and understory plant species and many types of wildlife, including other megaherbivores, smaller vertebrates, and arthropods. Our analysis indicates that elephants are not exerting profound negative effects on tree or herbivore species in the APNR, despite the sudden influx of elephants to newly opened territory in Thornybush in 2016 and heightened numbers of elephants in the other three unfenced reserves. A considerable number of kudu left Thornybush once the perimeter fences were removed, but we cannot determine whether they emigrated in response to elephants or to some other factor that was not measured by the APNR monitoring system.

The effects of elephants on ungulates have been less well studied than elephants' direct effects on trees, but our findings have important implications for biodiversity of herbivore guilds. Competitive exclusion by elephants, particularly from high value foraging resources and water sources could potentially induce severe limitations on the reproductive potential of other megaherbivores and smaller species. Further, predator restorations (intentional and unintentional) were carried out in the APNR reserves over the same time period in which elephants re-established occupancy. Successful restoration efforts might be hampered in circumstances where both megaherbivores and carnivores exert deleterious effects on patch availability. However, our analysis suggests that elephants have had little, if any, effect on three of the most abundant large herbivores in the APNR .

Previous studies in KNP and elsewhere have documented significant post reintroduction effects of elephants on marula trees, particularly the tallest and most mature individuals[134,159,160]. Marula trees are scarce in the APNR, so any loss of mature trees is conspicuous and may amplify the perception that marulas will eventually be extirpated on a given plot of land. Elephant presence has often been associated with increased marula mortality and a decline toward extirpation[134,159,161], seemingly at odds with their role as the primary vectors of seed dispersal for marulas[162] and the only herbivore with the bite force necessary to crush the strong integuments[142].

Long-standing exclosures in KNP provide some clues about why this happens[161]. Researchers documented high marula recruitment inside exclosures due to exclusion of impala, kudu, and other medium to large-bodied browsers that typically favor marula saplings[163]. Further, controlled fires within the exclosure indicated a higher tendency for marula seedlings to escape the fire trap absent pressure from ungulate herbivory. The fire escape height for marulas has been documented as 2.5-3 meters[164] and the height class most often impacted by elephants is the 5-8 meter height class[49], indicating that herbivory of saplings and young trees is the most important factor in limiting recruitment. This demonstrates the need to maintain diverse population structures of marulas, with trees in every height class and stage of its life cycle, which may require management interventions to protect young trees from browsers. Casual perceptions of elephant damage often overlook the importance of ongoing recruitment of smaller trees into the tallest height class. Thus, to actively promote rapid increases in marula trees, conservation managers should avoid culling elephants, which disrupts population dynamics[165], and instead pursue alternative mitigation strategies such as exclosures, chili fences[87], beehives[166], and wire netting[167].

FIGURES

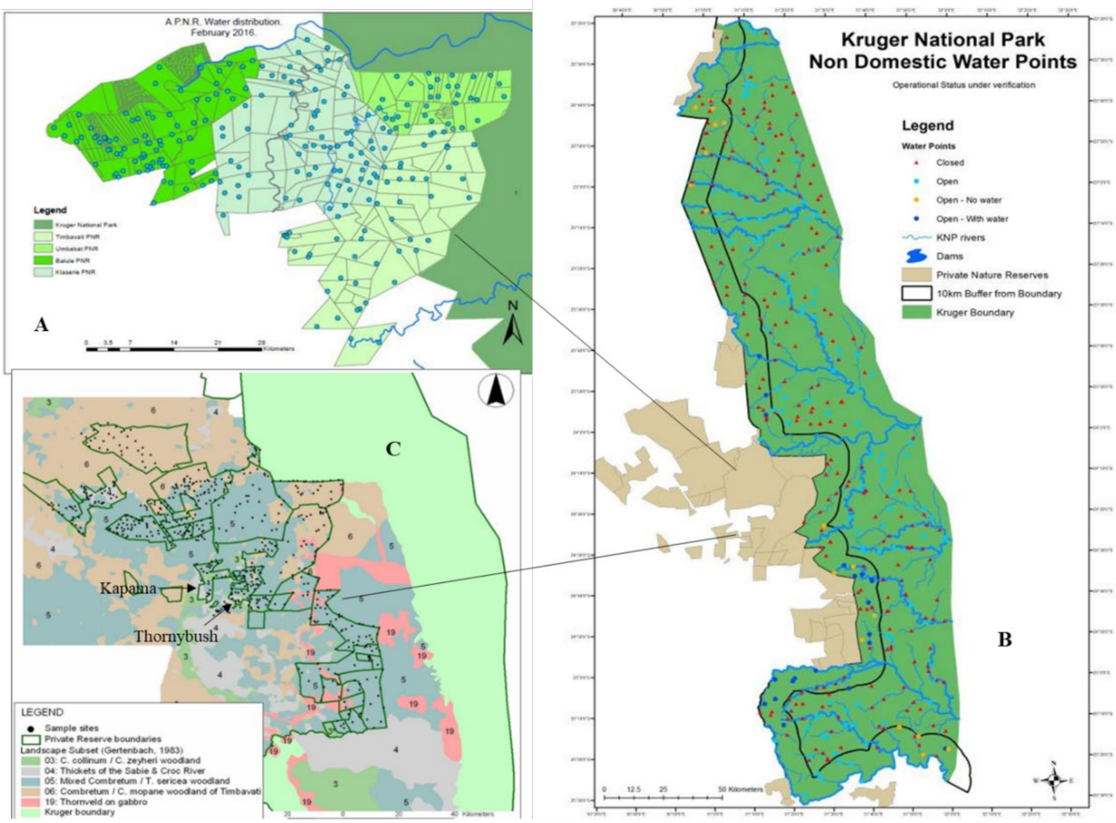

Figure 3.1. A) Map of open artificial waterholes at the Associated Private Nature Reserves. Note that when this map was created, Thornybush had not yet joined the APNR. Our study does not include data from Timbavati. **B**) Map of open (blue) and closed (red) boreholes at Kruger NP. The full complement of private reserves is shown here in tan. The black line signifies a 10 km boundary buffer between KNP and APNR. **C**) Map of the veld types in the APNR and partially into KNP. Black dots indicate the start of each transect.

Maps: A) Peel, APNR Management Report, 2015; B) Gaylard, 2015; C) Smit et al., 2007

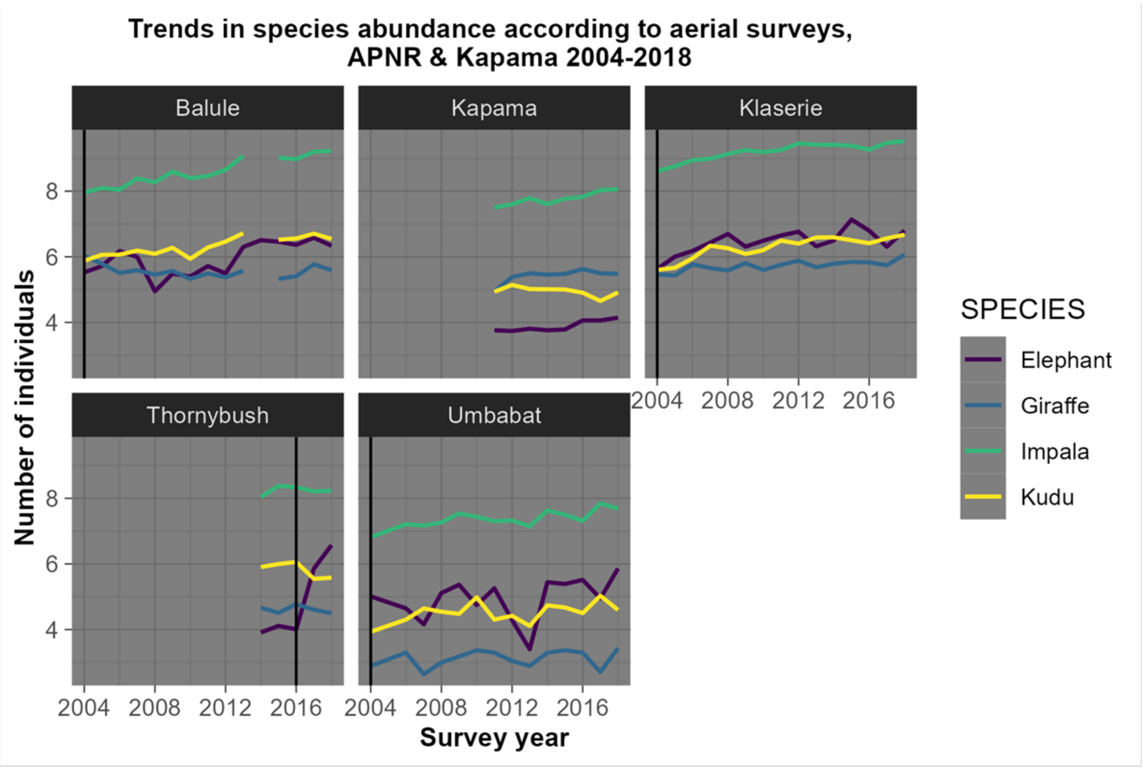

Figure 3.2. Trends in species abundance for four key browser species found at APNR and Kapama reserves. Aerial surveys began later at Kapama and Thornybush than the other three reserves, resulting in fewer data points. Black vertical lines indicate that fences were removed prior to the start of aerial surveys in three of the five reserves. Thornybush's fences were removed in 2016, and Kapama retains perimeter fencing.

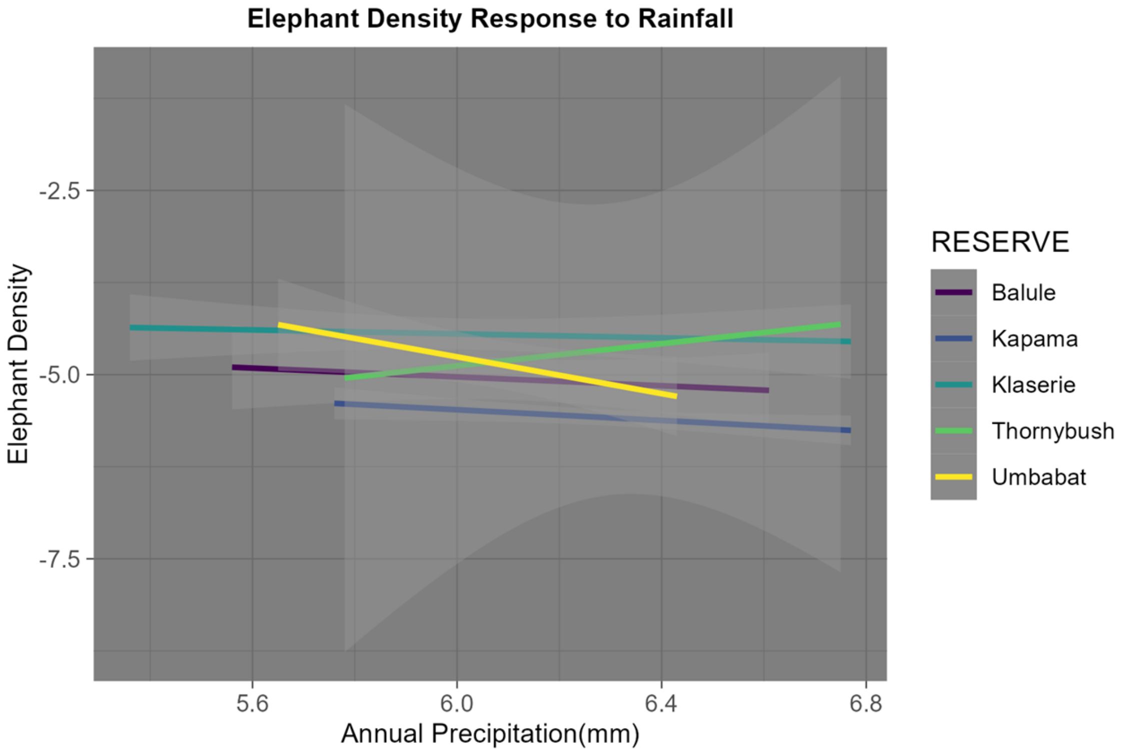

Figure 3.3 Elephant density trends vs annual rainfall, 2004-2018

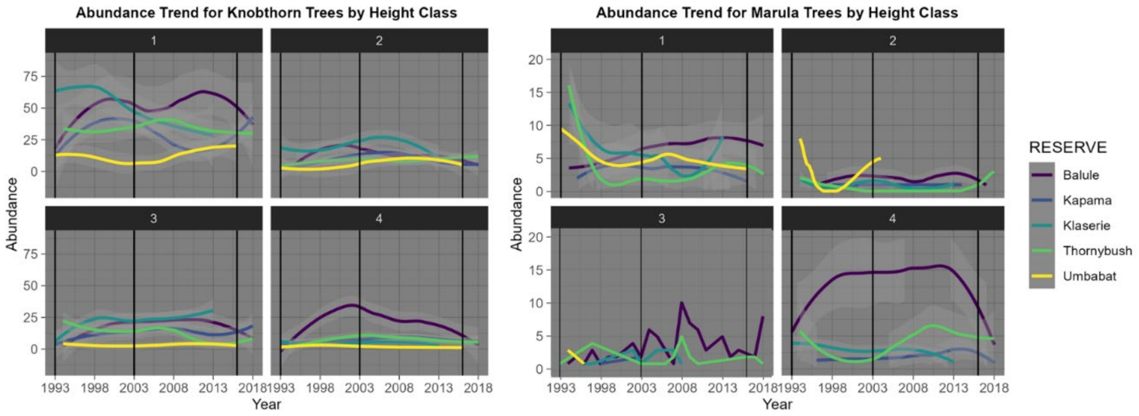

Figure 3.4 Abundance trends per height class across all five reserves for knobthorn and marula trees. Black vertical lines indicate when fences were removed in 1993, 2003, and 2016. Statistical analyses revealed no relationship with elephant density.

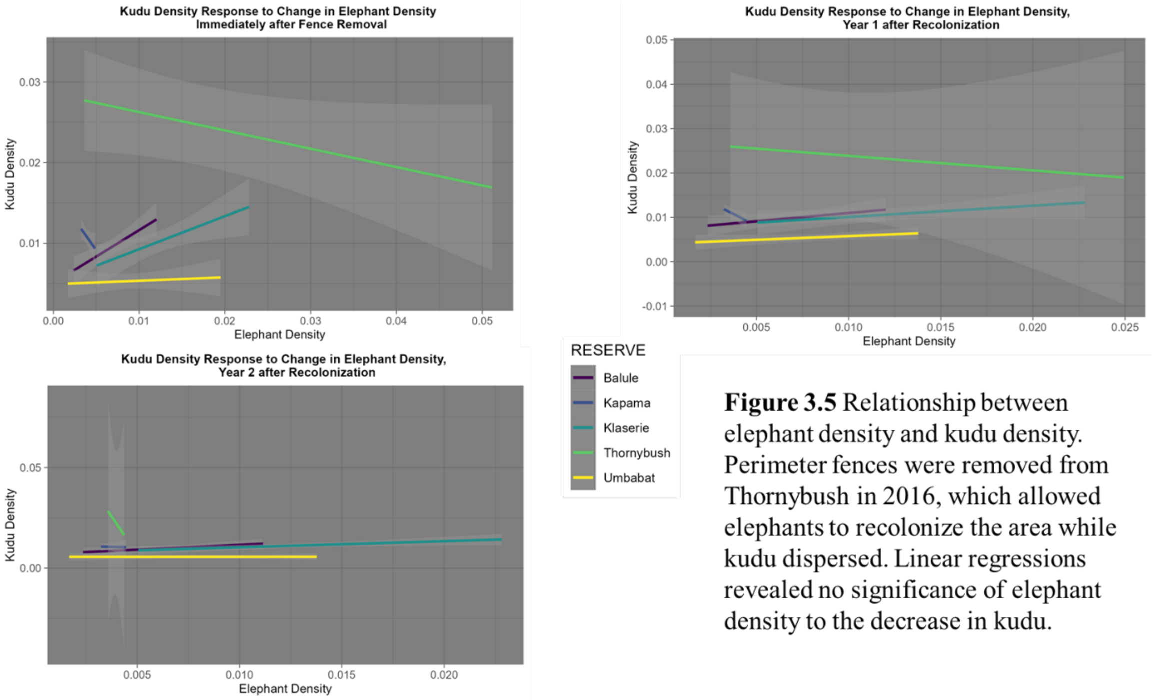

Figure 3.5 Relationship between elephant density and kudu density. Perimeter fences were removed from Thornybush in 2016, which allowed elephants to recolonize the area while kudu dispersed. Linear regressions revealed no significance of elephant density to the decrease in kudu.

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SUPPLEMENTARY MATERIALS

KAR

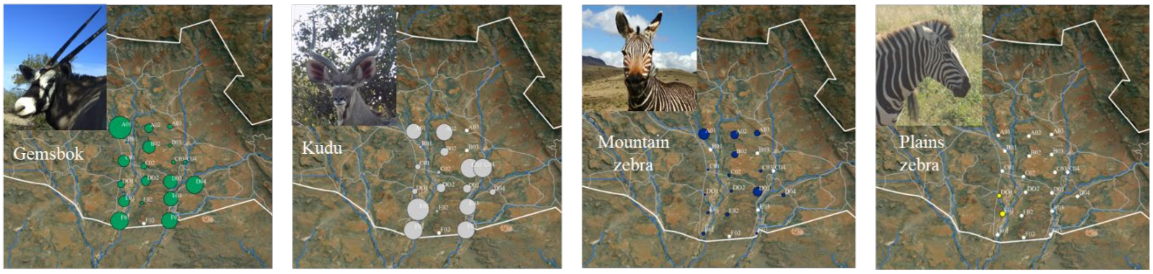

Figure 2.7a. GIS representations of how animals arrayed themselves across the CT grid in Karoo NP. Gemsbok are the most abundant species in the system according to both CTs and aerial surveys, and they were observed at every camera site within the grid. Kudu were underestimated by the CTs according to the aerial surveys. Karoo is the only site to have both mountain zebra and plains zebra—mountain zebra frequented every camera site while plains zebra were picked up only at two in a riparian area. The cameras are placed at high elevations on a plateau in this system.

MTZ

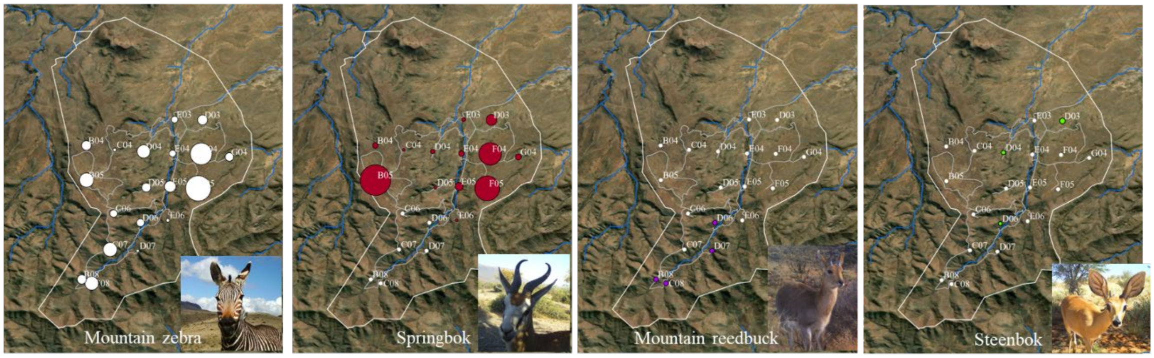

Figure 2.7b. GIS representations of how animals arrayed themselves across the CT grid in Mountain Zebra NP. Mountain zebra and springbok, the two most abundant species in this system, were captured at most camera sites, though springbok favored sites away from the river. The two least abundant species according to both survey methods—mountain reedbuck and steenbok—were only observed by 4 and 3 CTs, respectively.

PLN

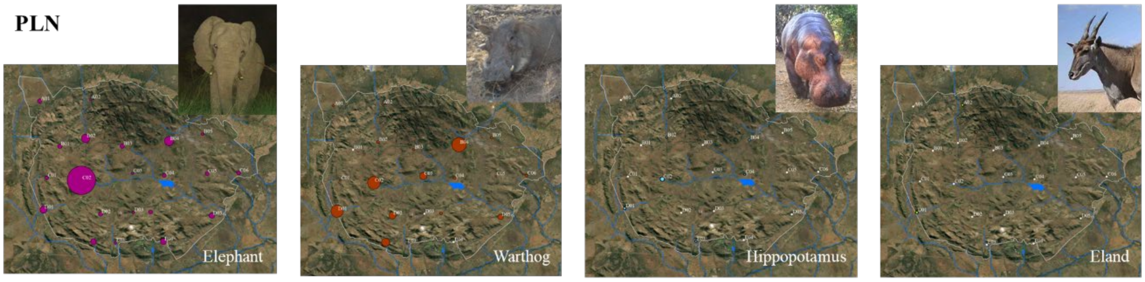

Figure 2.7c. GIS representations of how animals arrayed themselves across the CT grid in Pilanesberg NP. PLN has a large elephant and warthog populations, which used all of the sites but favored C02, which is on the end of a stream coming from a dam. Hippos were found only in sites with immediate access to water and most frequently at C02. Eland were only photographed at two sites, both on the rim of the crater.

Tables 3.1 – 3.8 Regression results from models of the effects of increasing elephant density on each height class of knobthorn trees one year and two years post elephant reintroduction.

Tables 3.9 – 3.16 Regression results for each height class of marula with one- and two-year lags after elephant density increased.

Tables 3.17 – 3.22 Regression results from modeling the effects of increasing elephant density on giraffe (3.17-18), impala (3.19-20), and kudu (3.21-22) density one year and two years after fence removal.

3.1. Knobthorn Height Class 1 (< 1m) Density One Year Post-Recolonization

	estimate	std.error	t.value	p.value
(Intercept)	0.006	0.007	0.902	0.380
ELE_DENSITY	-0.799	0.861	-0.929	0.367
RESERVEKapama	0.009	0.030	0.310	0.760
RESERVEKlaserie	-0.019	0.013	-1.461	0.163
RESERVEThornybush	-0.127	0.143	-0.890	0.387
RESERVEUmbabat	-0.009	0.018	-0.497	0.626
PRECIP	0.000	0.000	-0.866	0.399
ELE_DENSITY:RESERVEKapama	-4.184	7.990	-0.524	0.608
ELE_DENSITY:RESERVEKlaserie	1.396	1.226	1.138	0.272
ELE_DENSITY:RESERVEThornybush	31.517	36.350	0.867	0.399
ELE_DENSITY:RESERVEUmbabat	0.779	2.481	0.314	0.757
ELE_DENSITY:PRECIP	0.001	0.002	0.877	0.393
RESERVEKapama:PRECIP	0.000	0.000	-0.608	0.551
RESERVEKlaserie:PRECIP	0.000	0.000	1.675	0.113
RESERVEThornybush:PRECIP	0.000	0.000	0.896	0.383
RESERVEUmbabat:PRECIP	0.000	0.000	0.387	0.704
ELE_DENSITY:RESERVEKapama:PRECIP	0.013	0.017	0.805	0.433
ELE_DENSITY:RESERVEKlaserie:PRECIP	-0.004	0.002	-1.428	0.173
ELE_DENSITY:RESERVEThornybush:PRECIP	-0.049	0.056	-0.871	0.397
ELE_DENSITY:RESERVEUmbabat:PRECIP	-0.001	0.005	-0.173	0.865

3.2. Knobthorn Height Class 1 (< 1m) Density Two Years Post-Recolonization

	estimate	std.error	t.value	p.value
(Intercept)	-0.003	0.008	-0.358	0.727
ELE_DENSITY	0.394	1.059	0.372	0.717
RESERVEKapama	-0.031	0.052	-0.598	0.562
RESERVEKlaserie	0.105	0.066	1.600	0.138
RESERVEThornybush	-0.006	0.033	-0.186	0.855
RESERVEUmbabat	-0.024	0.048	-0.511	0.619
PRECIP	0.000	0.000	0.346	0.736
ELE_DENSITY:RESERVEKapama	10.408	15.838	0.657	0.525
ELE_DENSITY:RESERVEKlaserie	-12.809	7.887	-1.624	0.133
ELE_DENSITY:RESERVEThornybush	1.223	7.329	0.167	0.870
ELE_DENSITY:RESERVEUmbabat	-3.100	6.245	-0.496	0.629
ELE_DENSITY:PRECIP	-0.001	0.002	-0.406	0.693
RESERVEKapama:PRECIP	0.000	0.000	0.574	0.577
RESERVEKlaserie:PRECIP	0.000	0.000	-1.546	0.150
RESERVEThornybush:PRECIP	0.000	0.000	0.173	0.866
RESERVEUmbabat:PRECIP	0.000	0.000	0.509	0.621
ELE_DENSITY:RESERVEKapama:PRECIP	-0.030	0.052	-0.582	0.572
ELE_DENSITY:RESERVEKlaserie:PRECIP	0.032	0.020	1.566	0.146
ELE_DENSITY:RESERVEThornybush:PRECIP	NA	NA	NA	NA
ELE_DENSITY:RESERVEUmbabat:PRECIP	NA	NA	NA	NA

3.3. Knobthorn Height Class 2 (1-2 m) Density One Year Post-Recolonization

	estimate	std.error	t.value	p.value
(Intercept)	2.4E-05	2.6E-03	9.2E-03	9.9E-01
ELE_DENSITY	-3.8E-02	3.3E-01	-1.2E-01	9.1E-01
RESERVEKapama	-1.6E-02	1.2E-02	-1.4E+00	1.9E-01
RESERVEKlaserie	5.7E-03	5.0E-03	1.1E+00	2.7E-01
RESERVEThornybush	-1.7E-03	5.5E-02	-3.1E-02	9.8E-01
RESERVEUmbabat	-8.2E-03	6.8E-03	-1.2E+00	2.4E-01
PRECIP	-1.4E-07	5.0E-06	-2.7E-02	9.8E-01
ELE_DENSITY:RESERVEKapama	4.5E+00	3.1E+00	1.5E+00	1.6E-01
ELE_DENSITY:RESERVEKlaserie	-5.0E-01	4.7E-01	-1.1E+00	3.0E-01
ELE_DENSITY:RESERVEThornybush	1.5E-01	1.4E+01	1.1E-02	9.9E-01
ELE_DENSITY:RESERVEUmbabat	5.8E-01	9.5E-01	6.1E-01	5.5E-01
ELE_DENSITY:PRECIP	6.8E-05	6.5E-04	1.0E-01	9.2E-01
RESERVEKapama:PRECIP	3.3E-05	2.3E-05	1.4E+00	1.7E-01
RESERVEKlaserie:PRECIP	-1.1E-05	1.1E-05	-1.0E+00	3.3E-01
RESERVEThornybush:PRECIP	2.6E-06	8.2E-05	3.2E-02	9.8E-01
RESERVEUmbabat:PRECIP	1.8E-05	1.4E-05	1.3E+00	2.3E-01
ELE_DENSITY:RESERVEKapama:PRECIP	-9.6E-03	6.3E-03	-1.5E+00	1.5E-01
ELE_DENSITY:RESERVEKlaserie:PRECIP	9.1E-04	9.5E-04	9.6E-01	3.5E-01
ELE_DENSITY:RESERVEThornybush:PRECIP	-2.0E-04	2.1E-02	-9.2E-03	9.9E-01
ELE_DENSITY:RESERVEUmbabat:PRECIP	-1.0E-03	2.1E-03	-5.1E-01	6.2E-01

3.4. Knobthorn Height Class 2 (1-2 m) Density Two Years Post-Recolonization				
	estimate	std.error	t.value	p.value
(Intercept)	-0.002	0.002	-0.884	0.396
ELE_DENSITY	0.198	0.265	0.746	0.471
RESERVEKapama	-0.004	0.013	-0.320	0.755
RESERVEKlaserie	0.017	0.016	1.055	0.314
RESERVEThornybush	0.009	0.008	1.116	0.288
RESERVEUmbabat	-0.022	0.012	-1.829	0.095
PRECIP	0.000	0.000	0.767	0.459
ELE_DENSITY:RESERVEKapama	1.965	3.962	0.496	0.630
ELE_DENSITY:RESERVEKlaserie	-2.230	1.973	-1.130	0.282
ELE_DENSITY:RESERVEThornybush	-1.969	1.833	-1.074	0.306
ELE_DENSITY:RESERVEUmbabat	-2.769	1.562	-1.773	0.104
ELE_DENSITY:PRECIP	0.000	0.001	-0.688	0.506
RESERVEKapama:PRECIP	0.000	0.000	0.584	0.571
RESERVEKlaserie:PRECIP	0.000	0.000	-0.918	0.378
RESERVEThornybush:PRECIP	0.000	0.000	-0.867	0.405
RESERVEUmbabat:PRECIP	0.000	0.000	1.816	0.097
ELE_DENSITY:RESERVEKapama:PRECIP	-0.009	0.013	-0.658	0.524
ELE_DENSITY:RESERVEKlaserie:PRECIP	0.005	0.005	1.003	0.338
ELE_DENSITY:RESERVEThornybush:PRECIP	NA	NA	NA	NA
ELE_DENSITY:RESERVEUmbabat:PRECIP	NA	NA	NA	NA

3.5. Knobthorn Height Class 3 (2-5 m) Density One Year Post-Recolonization				
	estimate	std.error	t.value	p.value
(Intercept)	-3E-04	3E-03	-9E-02	9E-01
ELE_DENSITY	1E-02	4E-01	3E-02	1E+00
RESERVEKapama	2E-02	1E-02	1E+00	2E-01
RESERVEKlaserie	9E-04	5E-03	2E-01	9E-01
RESERVEThornybush	-5E-02	6E-02	-8E-01	4E-01
RESERVEUmbabat	3E-03	7E-03	4E-01	7E-01
PRECIP	1E-07	6E-06	2E-02	1E+00
ELE_DENSITY:RESERVEKapama	-5E+00	3E+00	-2E+00	1E-01
ELE_DENSITY:RESERVEKlaserie	-2E-01	5E-01	-4E-01	7E-01
ELE_DENSITY:RESERVEThornybush	1E+01	2E+01	8E-01	4E-01
ELE_DENSITY:RESERVEUmbabat	-6E-01	1E+00	-6E-01	5E-01
ELE_DENSITY:PRECIP	2E-05	7E-04	3E-02	1E+00
RESERVEKapama:PRECIP	-5E-05	2E-05	-2E+00	8E-02
RESERVEKlaserie:PRECIP	8E-07	1E-05	7E-02	9E-01
RESERVEThornybush:PRECIP	8E-05	9E-05	8E-01	4E-01
RESERVEUmbabat:PRECIP	-5E-06	2E-05	-3E-01	7E-01
ELE_DENSITY:RESERVEKapama:PRECIP	1E-02	7E-03	2E+00	5E-02
ELE_DENSITY:RESERVEKlaserie:PRECIP	2E-04	1E-03	2E-01	9E-01
ELE_DENSITY:RESERVEThornybush:PRECIP	-2E-02	2E-02	-8E-01	4E-01
ELE_DENSITY:RESERVEUmbabat:PRECIP	1E-03	2E-03	6E-01	6E-01

3.6. Knobthorn Height Class 3 (2-5 m) Density Two Years Post-Recolonization

	estimate	std.error	t.value	p.value
(Intercept)	-0.002	0.003	-0.607	0.556
ELE_DENSITY	0.276	0.451	0.613	0.552
RESERVEKapama	-0.016	0.022	-0.720	0.486
RESERVEKlaserie	0.017	0.028	0.591	0.566
RESERVEThornybush	0.006	0.014	0.447	0.664
RESERVEUmbabat	-0.003	0.020	-0.148	0.885
PRECIP	0.000	0.000	0.529	0.607
ELE_DENSITY:RESERVEKapama	4.293	6.738	0.637	0.537
ELE_DENSITY:RESERVEKlaserie	-2.196	3.355	-0.655	0.526
ELE_DENSITY:RESERVEThornybush	-1.349	3.118	-0.433	0.674
ELE_DENSITY:RESERVEUmbabat	-0.398	2.657	-0.150	0.884
ELE_DENSITY:PRECIP	-0.001	0.001	-0.584	0.571
RESERVEKapama:PRECIP	0.000	0.000	0.336	0.743
RESERVEKlaserie:PRECIP	0.000	0.000	-0.540	0.600
RESERVEThornybush:PRECIP	0.000	0.000	-0.287	0.779
RESERVEUmbabat:PRECIP	0.000	0.000	0.162	0.875
ELE_DENSITY:RESERVEKapama:PRECIP	-0.006	0.022	-0.294	0.774
ELE_DENSITY:RESERVEKlaserie:PRECIP	0.005	0.009	0.606	0.557
ELE_DENSITY:RESERVEThornybush:PRECIP	NA	NA	NA	NA
ELE_DENSITY:RESERVEUmbabat:PRECIP	NA	NA	NA	NA

3.7. Knobthorn Height Class 4 (>5 m) Density One Year Post-Recolonization

	estimate	std.error	t.value	p.value
(Intercept)	-4E-04	2E-03	-2E-01	8E-01
ELE_DENSITY	2E-03	2E-01	1E-02	1E+00
RESERVEKapama	-2E-02	8E-03	-2E+00	3E-02
RESERVEKlaserie	1E-03	3E-03	4E-01	7E-01
RESERVEThornybush	5E-02	4E-02	1E+00	2E-01
RESERVEUmbabat	-2E-03	5E-03	-4E-01	7E-01
PRECIP	8E-08	3E-06	2E-02	1E+00
ELE_DENSITY:RESERVEKapama	5E+00	2E+00	2E+00	3E-02
ELE_DENSITY:RESERVEKlaserie	-8E-02	3E-01	-2E-01	8E-01
ELE_DENSITY:RESERVEThornybush	-1E+01	9E+00	-1E+00	2E-01
ELE_DENSITY:RESERVEUmbabat	4E-01	6E-01	6E-01	6E-01
ELE_DENSITY:PRECIP	4E-05	4E-04	9E-02	9E-01
RESERVEKapama:PRECIP	3E-05	2E-05	2E+00	4E-02
RESERVEKlaserie:PRECIP	-2E-06	7E-06	-3E-01	7E-01
RESERVEThornybush:PRECIP	-7E-05	5E-05	-1E+00	2E-01
RESERVEUmbabat:PRECIP	5E-06	9E-06	5E-01	6E-01
ELE_DENSITY:RESERVEKapama:PRECIP	-9E-03	4E-03	-2E+00	5E-02
ELE_DENSITY:RESERVEKlaserie:PRECIP	1E-04	6E-04	2E-01	9E-01
ELE_DENSITY:RESERVEThornybush:PRECIP	2E-02	1E-02	1E+00	2E-01
ELE_DENSITY:RESERVEUmbabat:PRECIP	-9E-04	1E-03	-7E-01	5E-01

3.8. Knobthorn Height Class 4 (>5 m) Density Two Years Post-Recolonization

	estimate	std.error	t.value	p.value
(Intercept)	-0.003	0.003	-0.924	0.375
ELE_DENSITY	0.283	0.405	0.700	0.499
RESERVEKapama	-0.006	0.020	-0.311	0.761
RESERVEKlaserie	0.003	0.025	0.113	0.912
RESERVEThornybush	0.012	0.013	0.958	0.359
RESERVEUmbabat	0.002	0.018	0.085	0.934
PRECIP	0.000	0.000	0.778	0.453
ELE_DENSITY:RESERVEKapama	1.959	6.057	0.323	0.752
ELE_DENSITY:RESERVEKlaserie	-0.289	3.016	-0.096	0.925
ELE_DENSITY:RESERVEThornybush	-2.380	2.803	-0.849	0.414
ELE_DENSITY:RESERVEUmbabat	-0.098	2.388	-0.041	0.968
ELE_DENSITY:PRECIP	-0.001	0.001	-0.651	0.528
RESERVEKapama:PRECIP	0.000	0.000	0.119	0.907
RESERVEKlaserie:PRECIP	0.000	0.000	-0.060	0.953
RESERVEThornybush:PRECIP	0.000	0.000	-0.923	0.376
RESERVEUmbabat:PRECIP	0.000	0.000	-0.017	0.987
ELE_DENSITY:RESERVEKapama:PRECIP	-0.002	0.020	-0.125	0.903
ELE_DENSITY:RESERVEKlaserie:PRECIP	0.000	0.008	0.057	0.956
ELE_DENSITY:RESERVEThornybush:PRECIP	NA	NA	NA	NA
ELE_DENSITY:RESERVEUmbabat:PRECIP	NA	NA	NA	NA

3.9.Density of Marula Height Class 1 (< 1 m) One Year Post-Recolonization

	estimate	std.error	t.value	p.value
(Intercept)	6.7E-05	9.8E-04	6.9E-02	9.5E-01
ELE_DENSITY	-3.8E-02	1.2E-01	-3.1E-01	7.6E-01
RESERVEKapama	-4.4E-03	4.4E-03	-1.0E+00	3.3E-01
RESERVEKlaserie	-2.1E-03	1.9E-03	-1.1E+00	2.9E-01
RESERVEThornybush	1.1E-03	1.1E-03	1.0E+00	3.2E-01
RESERVEUmbabat	2.9E-04	4.0E-04	7.3E-01	4.7E-01
PRECIP	-4.8E-07	1.9E-06	-2.5E-01	8.0E-01
ELE_DENSITY:RESERVEKapama	9.9E-01	1.1E+00	8.6E-01	4.0E-01
ELE_DENSITY:RESERVEKlaserie	1.6E-01	1.8E-01	8.9E-01	3.9E-01
ELE_DENSITY:RESERVEThornybush	-1.3E-02	3.8E-02	-3.4E-01	7.4E-01
ELE_DENSITY:RESERVEUmbabat	NA	NA	NA	NA
ELE_DENSITY:PRECIP	1.3E-04	2.4E-04	5.2E-01	6.1E-01
RESERVEKapama:PRECIP	7.9E-06	8.5E-06	9.3E-01	3.7E-01
RESERVEKlaserie:PRECIP	4.1E-06	4.1E-06	1.0E+00	3.3E-01
RESERVEThornybush:PRECIP	-3.0E-06	2.5E-06	-1.2E+00	2.6E-01
RESERVEUmbabat:PRECIP	NA	NA	NA	NA
ELE_DENSITY:RESERVEKapama:PRECIP	-1.8E-03	2.4E-03	-7.6E-01	4.6E-01
ELE_DENSITY:RESERVEKlaserie:PRECIP	-3.2E-04	3.6E-04	-9.0E-01	3.8E-01
ELE_DENSITY:RESERVEThornybush:PRECIP	NA	NA	NA	NA
ELE_DENSITY:RESERVEUmbabat:PRECIP	NA	NA	NA	NA

3.10. Density of Marula Height Class 1 (< 1 m) Two Years Post-Recolonization

	estimate	std.error	t.value	p.value
(Intercept)	-0.002	0.001	-1.334	0.209
ELE_DENSITY	0.139	0.159	0.878	0.399
RESERVEKapama	0.001	0.008	0.176	0.863
RESERVEKlaserie	0.015	0.010	1.485	0.166
RESERVEThornybush	0.001	0.002	0.590	0.567
PRECIP	0.000	0.000	1.268	0.231
ELE_DENSITY:RESERVEKapama	-0.263	2.374	-0.111	0.914
ELE_DENSITY:RESERVEKlaserie	-1.745	1.182	-1.476	0.168
ELE_DENSITY:RESERVEThornybush	-0.068	0.243	-0.278	0.786
ELE_DENSITY:PRECIP	0.000	0.000	-0.807	0.437
RESERVEKapama:PRECIP	0.000	0.000	-0.194	0.850
RESERVEKlaserie:PRECIP	0.000	0.000	-1.546	0.150
RESERVEThornybush:PRECIP	0.000	0.000	-0.775	0.455
ELE_DENSITY:RESERVEKapama:PRECIP	0.001	0.008	0.139	0.892
ELE_DENSITY:RESERVEKlaserie:PRECIP	0.005	0.003	1.532	0.154
ELE_DENSITY:RESERVEThornybush:PRECIP	0.000	0.000	0.337	0.742

3.11. Density of Marula Height Class 2 (1-2 m) One Year Post-Recolonization

	estimate	std.error	t.value	p.value
(Intercept)	7E-05	3E-04	2E-01	8E-01
ELE_DENSITY	-1E-02	4E-02	-3E-01	8E-01
RESERVEKapama	1E-03	2E-03	9E-01	4E-01
RESERVEKlaserie	7E-05	7E-04	1E-01	9E-01
RESERVEThornybush	-3E-04	2E-04	-1E+00	2E-01
RESERVEUmbabat	-9E-04	1E-04	-6E+00	1E-05
PRECIP	-5E-08	7E-07	-7E-02	9E-01
ELE_DENSITY:RESERVEKapama	-3E-01	4E-01	-8E-01	4E-01
ELE_DENSITY:RESERVEKlaserie	6E-03	6E-02	1E-01	9E-01
ELE_DENSITY:RESERVEThornybush	3E-02	2E-02	2E+00	1E-01
ELE_DENSITY:RESERVEUmbabat	NA	NA	NA	NA
ELE_DENSITY:PRECIP	1E-05	9E-05	1E-01	9E-01
RESERVEKapama:PRECIP	-3E-06	3E-06	-9E-01	4E-01
RESERVEKlaserie:PRECIP	-6E-07	1E-06	-4E-01	7E-01
RESERVEThornybush:PRECIP	NA	NA	NA	NA
RESERVEUmbabat:PRECIP	NA	NA	NA	NA
ELE_DENSITY:RESERVEKapama:PRECIP	7E-04	8E-04	8E-01	4E-01
ELE_DENSITY:RESERVEKlaserie:PRECIP	3E-05	1E-04	2E-01	8E-01
ELE_DENSITY:RESERVEThornybush:PRECIP	NA	NA	NA	NA
ELE_DENSITY:RESERVEUmbabat:PRECIP	NA	NA	NA	NA

3.12. Density of Marula Height Class 2 (1-2 m) Two Years Post-Recolonization

	estimate	std.error	t.value	p.value
(Intercept)	-2E-04	4E-04	-5E-01	6E-01
ELE_DENSITY	2E-02	5E-02	4E-01	7E-01
RESERVEKapama	4E-05	2E-03	2E-02	1E+00
RESERVEKlaserie	-8E-04	3E-03	-3E-01	8E-01
RESERVEThornybush	-3E-03	3E-03	-1E+00	3E-01
PRECIP	5E-07	7E-07	8E-01	5E-01
ELE_DENSITY:RESERVEKapama	6E-03	7E-01	9E-03	1E+00
ELE_DENSITY:RESERVEKlaserie	1E-01	4E-01	3E-01	8E-01
ELE_DENSITY:RESERVEThornybush	9E-01	8E-01	1E+00	3E-01
ELE_DENSITY:PRECIP	-6E-05	9E-05	-7E-01	5E-01
RESERVEKapama:PRECIP	-8E-07	8E-06	-1E-01	9E-01
RESERVEKlaserie:PRECIP	2E-06	8E-06	2E-01	8E-01
RESERVEThornybush:PRECIP	NA	NA	NA	NA
ELE_DENSITY:RESERVEKapama:PRECIP	2E-04	2E-03	7E-02	9E-01
ELE_DENSITY:RESERVEKlaserie:PRECIP	-2E-04	9E-04	-2E-01	8E-01
ELE_DENSITY:RESERVEThornybush:PRECIP	NA	NA	NA	NA

3.13. Density of Marula Height Class 3 (2-5 m) One Year Post-Recolonization

	estimate	std.error	t.value	p.value
(Intercept)	-0.002	0.003	-0.679	0.507
ELE_DENSITY	0.188	0.360	0.524	0.608
RESERVEKapama	0.002	0.013	0.152	0.881
RESERVEKlaserie	0.001	0.005	0.154	0.879
RESERVEThornybush	0.000	0.002	0.256	0.801
RESERVEUmbabat	0.002	0.009	0.208	0.838
PRECIP	0.000	0.000	0.685	0.503
ELE_DENSITY:RESERVEKapama	-0.188	3.337	-0.056	0.956
ELE_DENSITY:RESERVEKlaserie	-0.142	0.512	-0.277	0.785
ELE_DENSITY:RESERVEThornybush	0.005	0.151	0.034	0.973
ELE_DENSITY:RESERVEUmbabat	-0.188	0.779	-0.242	0.812
ELE_DENSITY:PRECIP	0.000	0.001	-0.513	0.615
RESERVEKapama:PRECIP	0.000	0.000	-0.153	0.880
RESERVEKlaserie:PRECIP	0.000	0.000	-0.026	0.980
RESERVEThornybush:PRECIP	NA	NA	NA	NA
RESERVEUmbabat:PRECIP	0.000	0.000	-0.223	0.826
ELE_DENSITY:RESERVEKapama:PRECIP	0.000	0.007	0.053	0.959
ELE_DENSITY:RESERVEKlaserie:PRECIP	0.000	0.001	0.165	0.871
ELE_DENSITY:RESERVEThornybush:PRECIP	NA	NA	NA	NA
ELE_DENSITY:RESERVEUmbabat:PRECIP	0.000	0.002	0.237	0.815

3.14. Density of Marula Height Class 3 (2-5 m) Two Years Post-Recolonization				
	estimate	std.error	t.value	p.value
(Intercept)	-0.004	0.002	-1.703	0.114
ELE_DENSITY	0.392	0.294	1.331	0.208
RESERVEKapama	0.004	0.014	0.266	0.795
RESERVEKlaserie	0.007	0.018	0.396	0.699
RESERVEThornybush	-0.016	0.019	-0.839	0.418
RESERVEUmbabat	0.004	0.007	0.537	0.601
PRECIP	0.000	0.000	1.402	0.186
ELE_DENSITY:RESERVEKapama	-0.392	4.397	-0.089	0.931
ELE_DENSITY:RESERVEKlaserie	-0.839	2.190	-0.383	0.708
ELE_DENSITY:RESERVEThornybush	4.240	4.943	0.858	0.408
ELE_DENSITY:RESERVEUmbabat	-0.392	0.603	-0.649	0.528
ELE_DENSITY:PRECIP	-0.001	0.001	-1.081	0.301
RESERVEKapama:PRECIP	0.000	0.000	-0.129	0.900
RESERVEKlaserie:PRECIP	0.000	0.000	-0.298	0.771
RESERVEThornybush:PRECIP	NA	NA	NA	NA
RESERVEUmbabat:PRECIP	0.000	0.000	-0.464	0.651
ELE_DENSITY:RESERVEKapama:PRECIP	0.001	0.014	0.042	0.967
ELE_DENSITY:RESERVEKlaserie:PRECIP	0.002	0.006	0.293	0.775
ELE_DENSITY:RESERVEThornybush:PRECIP	NA	NA	NA	NA
ELE_DENSITY:RESERVEUmbabat:PRECIP	0.001	0.001	0.513	0.617

3.15. Density of Marula Height Class 4 (>5 m) One Year Post-Recolonization				
	estimate	std.error	t.value	p.value
(Intercept)	-0.001	0.001	-0.993	0.338
ELE_DENSITY	0.108	0.159	0.676	0.510
RESERVEKapama	-0.009	0.008	-1.047	0.313
RESERVEKlaserie	0.001	0.002	0.555	0.588
RESERVEThornybush	0.000	0.001	0.642	0.531
RESERVEUmbabat	0.000	0.001	0.149	0.883
PRECIP	0.000	0.000	0.921	0.373
ELE_DENSITY:RESERVEKapama	3.289	2.561	1.285	0.220
ELE_DENSITY:RESERVEKlaserie	-0.117	0.227	-0.517	0.614
ELE_DENSITY:RESERVEThornybush	0.014	0.067	0.207	0.839
ELE_DENSITY:RESERVEUmbabat	NA	NA	NA	NA
ELE_DENSITY:PRECIP	0.000	0.000	-0.669	0.515
RESERVEKapama:PRECIP	0.000	0.000	1.591	0.134
RESERVEKlaserie:PRECIP	0.000	0.000	-0.467	0.648
RESERVEThornybush:PRECIP	NA	NA	NA	NA
RESERVEUmbabat:PRECIP	NA	NA	NA	NA
ELE_DENSITY:RESERVEKapama:PRECIP	-0.014	0.008	-1.669	0.117
ELE_DENSITY:RESERVEKlaserie:PRECIP	0.000	0.000	0.516	0.614
ELE_DENSITY:RESERVEThornybush:PRECIP	NA	NA	NA	NA
ELE_DENSITY:RESERVEUmbabat:PRECIP	NA	NA	NA	NA

3.16. Density of Marula Height Class 4 (>5 m) Two Years Post-Recolonization

	estimate	std.error	t.value	p.value
(Intercept)	-0.001	0.002	-0.803	0.439
ELE_DENSITY	0.110	0.242	0.454	0.659
RESERVEKapama	0.002	0.012	0.208	0.839
RESERVEKlaserie	0.001	0.015	0.098	0.923
RESERVEThornybush	-0.018	0.015	-1.150	0.275
PRECIP	0.000	0.000	0.660	0.523
ELE_DENSITY:RESERVEKapama	-0.389	3.618	-0.107	0.916
ELE_DENSITY:RESERVEKlaserie	-0.110	1.802	-0.061	0.952
ELE_DENSITY:RESERVEThornybush	4.761	4.067	1.171	0.267
ELE_DENSITY:PRECIP	0.000	0.000	-0.442	0.667
RESERVEKapama:PRECIP	0.000	0.000	0.031	0.976
RESERVEKlaserie:PRECIP	0.000	0.000	-0.059	0.954
RESERVEThornybush:PRECIP	NA	NA	NA	NA
ELE_DENSITY:RESERVEKapama:PRECIP	-0.001	0.012	-0.071	0.945
ELE_DENSITY:RESERVEKlaserie:PRECIP	0.000	0.005	0.044	0.966
ELE_DENSITY:RESERVEThornybush:PRECIP	NA	NA	NA	NA

3.17. Giraffe Density One Year Post-Recolonization

	estimate	std.error	t.value	p.value
(Intercept)	-0.028	0.108	-0.261	0.796
ELE_DENSITY	4.009	13.312	0.301	0.765
PRECIP	0.000	0.000	0.272	0.787
AVG_SHADE	0.002	0.062	0.029	0.977
AVG_DIST_TREES	0.001	0.001	0.530	0.600
RESERVEKapama	-0.006	0.062	-0.098	0.922
RESERVEKlaserie	NA	NA	NA	NA
RESERVEUmbabat	NA	NA	NA	NA
ELE_DENSITY:PRECIP	-0.009	0.030	-0.303	0.764
ELE_DENSITY:AVG_SHADE	-1.190	6.031	-0.197	0.845
PRECIP:AVG_SHADE	0.000	0.000	-0.012	0.991
ELE_DENSITY:AVG_DIST_TREES	-0.056	0.148	-0.378	0.708
PRECIP:AVG_DIST_TREES	0.000	0.000	-0.518	0.608
AVG_SHADE:AVG_DIST_TREES	NA	NA	NA	NA
ELE_DENSITY:RESERVEKapama	1.202	15.405	0.078	0.938
ELE_DENSITY:RESERVEKlaserie	NA	NA	NA	NA
ELE_DENSITY:RESERVEUmbabat	NA	NA	NA	NA
PRECIP:RESERVEKapama	0.000	0.000	0.523	0.605
PRECIP:RESERVEKlaserie	NA	NA	NA	NA
PRECIP:RESERVEUmbabat	NA	NA	NA	NA
AVG_SHADE:RESERVEKapama	NA	NA	NA	NA
AVG_SHADE:RESERVEKlaserie	NA	NA	NA	NA
AVG_SHADE:RESERVEUmbabat	NA	NA	NA	NA
AVG_DIST_TREES:RESERVEKapama	NA	NA	NA	NA
AVG_DIST_TREES:RESERVEKlaserie	NA	NA	NA	NA
AVG_DIST_TREES:RESERVEUmbabat	NA	NA	NA	NA
ELE_DENSITY:PRECIP:AVG_SHADE	0.003	0.013	0.205	0.839
ELE_DENSITY:PRECIP:AVG_DIST_TREES	0.000	0.000	0.373	0.712
ELE_DENSITY:AVG_SHADE:AVG_DIST_TREES	NA	NA	NA	NA
PRECIP:AVG_SHADE:AVG_DIST_TREES	NA	NA	NA	NA
ELE_DENSITY:PRECIP:RESERVEKapama	-0.015	0.032	-0.483	0.633
ELE_DENSITY:PRECIP:RESERVEKlaserie	NA	NA	NA	NA
ELE_DENSITY:PRECIP:RESERVEUmbabat	NA	NA	NA	NA
ELE_DENSITY:AVG_SHADE:RESERVEKapama	NA	NA	NA	NA
ELE_DENSITY:AVG_SHADE:RESERVEKlaserie	NA	NA	NA	NA
ELE_DENSITY:AVG_SHADE:RESERVEUmbabat	NA	NA	NA	NA
PRECIP:AVG_SHADE:RESERVEKapama	NA	NA	NA	NA
PRECIP:AVG_SHADE:RESERVEKlaserie	NA	NA	NA	NA
PRECIP:AVG_SHADE:RESERVEUmbabat	NA	NA	NA	NA
ELE_DENSITY:AVG_DIST_TREES:RESERVEKapama	NA	NA	NA	NA
ELE_DENSITY:AVG_DIST_TREES:RESERVEKlaserie	NA	NA	NA	NA
ELE_DENSITY:AVG_DIST_TREES:RESERVEUmbabat	NA	NA	NA	NA
PRECIP:AVG_DIST_TREES:RESERVEKapama	NA	NA	NA	NA
PRECIP:AVG_DIST_TREES:RESERVEKlaserie	NA	NA	NA	NA
PRECIP:AVG_DIST_TREES:RESERVEUmbabat	NA	NA	NA	NA
AVG_SHADE:AVG_DIST_TREES:RESERVEKapama	NA	NA	NA	NA
AVG_SHADE:AVG_DIST_TREES:RESERVEKlaserie	NA	NA	NA	NA
AVG_SHADE:AVG_DIST_TREES:RESERVEUmbabat	NA	NA	NA	NA
ELE_DENSITY:PRECIP:AVG_SHADE:AVG_DIST_TREES	NA	NA	NA	NA
ELE_DENSITY:PRECIP:AVG_SHADE:RESERVEKapama	NA	NA	NA	NA
ELE_DENSITY:PRECIP:AVG_SHADE:RESERVEKlaserie	NA	NA	NA	NA
ELE_DENSITY:PRECIP:AVG_SHADE:RESERVEUmbabat	NA	NA	NA	NA
ELE_DENSITY:PRECIP:AVG_DIST_TREES:RESERVEKapama	NA	NA	NA	NA
ELE_DENSITY:PRECIP:AVG_DIST_TREES:RESERVEKlaserie	NA	NA	NA	NA
ELE_DENSITY:PRECIP:AVG_DIST_TREES:RESERVEUmbabat	NA	NA	NA	NA
ELE_DENSITY:AVG_SHADE:AVG_DIST_TREES:RESERVEKapama	NA	NA	NA	NA
ELE_DENSITY:AVG_SHADE:AVG_DIST_TREES:RESERVEKlaserie	NA	NA	NA	NA
ELE_DENSITY:AVG_SHADE:AVG_DIST_TREES:RESERVEUmbabat	NA	NA	NA	NA
PRECIP:AVG_SHADE:AVG_DIST_TREES:RESERVEKapama	NA	NA	NA	NA
PRECIP:AVG_SHADE:AVG_DIST_TREES:RESERVEKlaserie	NA	NA	NA	NA
PRECIP:AVG_SHADE:AVG_DIST_TREES:RESERVEUmbabat	NA	NA	NA	NA
ELE_DENSITY:PRECIP:AVG_SHADE:AVG_DIST_TREES:RESERVEKapama	NA	NA	NA	NA
ELE_DENSITY:PRECIP:AVG_SHADE:AVG_DIST_TREES:RESERVEKlaserie	NA	NA	NA	NA
ELE_DENSITY:PRECIP:AVG_SHADE:AVG_DIST_TREES:RESERVEUmbabat	NA	NA	NA	NA

3.18. Giraffe Density Two Years Post-Recolonization

	estimate	std.error	t.value	p.value
(Intercept)	-0.037	0.119	-0.309	0.760
ELE_DENSITY	5.665	13.566	0.418	0.680
PRECIP	0.000	0.000	0.284	0.778
AVG_SHADE	0.017	0.064	0.265	0.793
AVG_DIST_TREES	0.000	0.002	0.100	0.921
RESERVEKapama	0.187	0.089	2.108	0.045
RESERVEKlaserie	NA	NA	NA	NA
RESERVEUmbabat	NA	NA	NA	NA
ELE_DENSITY:PRECIP	-0.011	0.029	-0.377	0.709
ELE_DENSITY:AVG_SHADE	-2.565	6.083	-0.422	0.677
PRECIP:AVG_SHADE	0.000	0.000	-0.365	0.718
ELE_DENSITY:AVG_DIST_TREES	-0.025	0.151	-0.164	0.871
PRECIP:AVG_DIST_TREES	0.000	0.000	0.137	0.892
AVG_SHADE:AVG_DIST_TREES	NA	NA	NA	NA
ELE_DENSITY:RESERVEKapama	-50.705	26.371	-1.923	0.066
ELE_DENSITY:RESERVEKlaserie	NA	NA	NA	NA
ELE_DENSITY:RESERVEUmbabat	NA	NA	NA	NA
PRECIP:RESERVEKapama	0.000	0.000	-1.481	0.151
PRECIP:RESERVEKlaserie	NA	NA	NA	NA
PRECIP:RESERVEUmbabat	NA	NA	NA	NA
AVG_SHADE:RESERVEKapama	NA	NA	NA	NA
AVG_SHADE:RESERVEKlaserie	NA	NA	NA	NA
AVG_SHADE:RESERVEUmbabat	NA	NA	NA	NA
AVG_DIST_TREES:RESERVEKapama	NA	NA	NA	NA
AVG_DIST_TREES:RESERVEKlaserie	NA	NA	NA	NA
AVG_DIST_TREES:RESERVEUmbabat	NA	NA	NA	NA
ELE_DENSITY:PRECIP:AVG_SHADE	0.006	0.013	0.495	0.625
ELE_DENSITY:PRECIP:AVG_DIST_TREES	0.000	0.000	-0.048	0.962
ELE_DENSITY:AVG_SHADE:AVG_DIST_TREES	NA	NA	NA	NA
PRECIP:AVG_SHADE:AVG_DIST_TREES	NA	NA	NA	NA
ELE_DENSITY:PRECIP:RESERVEKapama	0.117	0.086	1.360	0.185
ELE_DENSITY:PRECIP:RESERVEKlaserie	NA	NA	NA	NA
ELE_DENSITY:PRECIP:RESERVEUmbabat	NA	NA	NA	NA
ELE_DENSITY:AVG_SHADE:RESERVEKapama	NA	NA	NA	NA
ELE_DENSITY:AVG_SHADE:RESERVEKlaserie	NA	NA	NA	NA
ELE_DENSITY:AVG_SHADE:RESERVEUmbabat	NA	NA	NA	NA
PRECIP:AVG_SHADE:RESERVEKapama	NA	NA	NA	NA
PRECIP:AVG_SHADE:RESERVEKlaserie	NA	NA	NA	NA
PRECIP:AVG_SHADE:RESERVEUmbabat	NA	NA	NA	NA
ELE_DENSITY:AVG_DIST_TREES:RESERVEKapama	NA	NA	NA	NA
ELE_DENSITY:AVG_DIST_TREES:RESERVEKlaserie	NA	NA	NA	NA
ELE_DENSITY:AVG_DIST_TREES:RESERVEUmbabat	NA	NA	NA	NA
PRECIP:AVG_DIST_TREES:RESERVEKapama	NA	NA	NA	NA
PRECIP:AVG_DIST_TREES:RESERVEKlaserie	NA	NA	NA	NA
PRECIP:AVG_DIST_TREES:RESERVEUmbabat	NA	NA	NA	NA
AVG_SHADE:AVG_DIST_TREES:RESERVEKapama	NA	NA	NA	NA
AVG_SHADE:AVG_DIST_TREES:RESERVEKlaserie	NA	NA	NA	NA
AVG_SHADE:AVG_DIST_TREES:RESERVEUmbabat	NA	NA	NA	NA
ELE_DENSITY:PRECIP:AVG_SHADE:AVG_DIST_TREES	NA	NA	NA	NA
ELE_DENSITY:PRECIP:AVG_SHADE:RESERVEKapama	NA	NA	NA	NA
ELE_DENSITY:PRECIP:AVG_SHADE:RESERVEKlaserie	NA	NA	NA	NA
ELE_DENSITY:PRECIP:AVG_SHADE:RESERVEUmbabat	NA	NA	NA	NA
ELE_DENSITY:PRECIP:AVG_DIST_TREES:RESERVEKapama	NA	NA	NA	NA
ELE_DENSITY:PRECIP:AVG_DIST_TREES:RESERVEKlaserie	NA	NA	NA	NA
ELE_DENSITY:PRECIP:AVG_DIST_TREES:RESERVEUmbabat	NA	NA	NA	NA
ELE_DENSITY:AVG_SHADE:AVG_DIST_TREES:RESERVEKapama	NA	NA	NA	NA
ELE_DENSITY:AVG_SHADE:AVG_DIST_TREES:RESERVEKlaserie	NA	NA	NA	NA
ELE_DENSITY:AVG_SHADE:AVG_DIST_TREES:RESERVEUmbabat	NA	NA	NA	NA
PRECIP:AVG_SHADE:AVG_DIST_TREES:RESERVEKapama	NA	NA	NA	NA
PRECIP:AVG_SHADE:AVG_DIST_TREES:RESERVEKlaserie	NA	NA	NA	NA
PRECIP:AVG_SHADE:AVG_DIST_TREES:RESERVEUmbabat	NA	NA	NA	NA
ELE_DENSITY:PRECIP:AVG_SHADE:AVG_DIST_TREES:RESERVEKapama	NA	NA	NA	NA
ELE_DENSITY:PRECIP:AVG_SHADE:AVG_DIST_TREES:RESERVEKlaserie	NA	NA	NA	NA
ELE_DENSITY:PRECIP:AVG_SHADE:AVG_DIST_TREES:RESERVEUmbabat	NA	NA	NA	NA

3.19. Impala Density One Year Post-Recolonization

	estimate	std.error	t.value	p.value
(Intercept)	-0.323	1.637	-0.197	0.845
ELE_DENSITY	40.741	201.433	0.202	0.841
PRECIP	0.001	0.003	0.373	0.712
AVG_SHADE	-0.109	0.932	-0.117	0.908
AVG_DIST_TREES	0.016	0.021	0.761	0.453
RESERVEKapama	-0.785	0.935	-0.840	0.408
RESERVEKlaserie	NA	NA	NA	NA
RESERVEUmbabat	NA	NA	NA	NA
ELE_DENSITY:PRECIP	-0.151	0.450	-0.336	0.739
ELE_DENSITY:AVG_SHADE	-7.220	91.263	-0.079	0.937
PRECIP:AVG_SHADE	0.000	0.002	0.012	0.991
ELE_DENSITY:AVG_DIST_TREES	-0.916	2.234	-0.410	0.685
PRECIP:AVG_DIST_TREES	0.000	0.000	-0.825	0.416
AVG_SHADE:AVG_DIST_TREES	NA	NA	NA	NA
ELE_DENSITY:RESERVEKapama	179.961	233.096	0.772	0.446
ELE_DENSITY:RESERVEKlaserie	NA	NA	NA	NA
ELE_DENSITY:RESERVEUmbabat	NA	NA	NA	NA
PRECIP:RESERVEKapama	0.001	0.002	0.761	0.452
PRECIP:RESERVEKlaserie	NA	NA	NA	NA
PRECIP:RESERVEUmbabat	NA	NA	NA	NA
AVG_SHADE:RESERVEKapama	NA	NA	NA	NA
AVG_SHADE:RESERVEKlaserie	NA	NA	NA	NA
AVG_SHADE:RESERVEUmbabat	NA	NA	NA	NA
AVG_DIST_TREES:RESERVEKapama	NA	NA	NA	NA
AVG_DIST_TREES:RESERVEKlaserie	NA	NA	NA	NA
AVG_DIST_TREES:RESERVEUmbabat	NA	NA	NA	NA
ELE_DENSITY:PRECIP:AVG_SHADE	0.048	0.193	0.246	0.807
ELE_DENSITY:PRECIP:AVG_DIST_TREES	0.002	0.005	0.455	0.652
ELE_DENSITY:AVG_SHADE:AVG_DIST_TREES	NA	NA	NA	NA
PRECIP:AVG_SHADE:AVG_DIST_TREES	NA	NA	NA	NA
ELE_DENSITY:PRECIP:RESERVEKapama	-0.297	0.484	-0.613	0.545
ELE_DENSITY:PRECIP:RESERVEKlaserie	NA	NA	NA	NA
ELE_DENSITY:PRECIP:RESERVEUmbabat	NA	NA	NA	NA
ELE_DENSITY:AVG_SHADE:RESERVEKapama	NA	NA	NA	NA
ELE_DENSITY:AVG_SHADE:RESERVEKlaserie	NA	NA	NA	NA
ELE_DENSITY:AVG_SHADE:RESERVEUmbabat	NA	NA	NA	NA
PRECIP:AVG_SHADE:RESERVEKapama	NA	NA	NA	NA
PRECIP:AVG_SHADE:RESERVEKlaserie	NA	NA	NA	NA
PRECIP:AVG_SHADE:RESERVEUmbabat	NA	NA	NA	NA
ELE_DENSITY:AVG_DIST_TREES:RESERVEKapama	NA	NA	NA	NA
ELE_DENSITY:AVG_DIST_TREES:RESERVEKlaserie	NA	NA	NA	NA
ELE_DENSITY:AVG_DIST_TREES:RESERVEUmbabat	NA	NA	NA	NA
PRECIP:AVG_DIST_TREES:RESERVEKapama	NA	NA	NA	NA
PRECIP:AVG_DIST_TREES:RESERVEKlaserie	NA	NA	NA	NA
PRECIP:AVG_DIST_TREES:RESERVEUmbabat	NA	NA	NA	NA
AVG_SHADE:AVG_DIST_TREES:RESERVEKapama	NA	NA	NA	NA
AVG_SHADE:AVG_DIST_TREES:RESERVEKlaserie	NA	NA	NA	NA
AVG_SHADE:AVG_DIST_TREES:RESERVEUmbabat	NA	NA	NA	NA
ELE_DENSITY:PRECIP:AVG_SHADE:AVG_DIST_TREES	NA	NA	NA	NA
ELE_DENSITY:PRECIP:AVG_SHADE:RESERVEKapama	NA	NA	NA	NA
ELE_DENSITY:PRECIP:AVG_SHADE:RESERVEKlaserie	NA	NA	NA	NA
ELE_DENSITY:PRECIP:AVG_SHADE:RESERVEUmbabat	NA	NA	NA	NA
ELE_DENSITY:PRECIP:AVG_DIST_TREES:RESERVEKapama	NA	NA	NA	NA
ELE_DENSITY:PRECIP:AVG_DIST_TREES:RESERVEKlaserie	NA	NA	NA	NA
ELE_DENSITY:PRECIP:AVG_DIST_TREES:RESERVEUmbabat	NA	NA	NA	NA
ELE_DENSITY:AVG_SHADE:AVG_DIST_TREES:RESERVEKapama	NA	NA	NA	NA
ELE_DENSITY:AVG_SHADE:AVG_DIST_TREES:RESERVEKlaserie	NA	NA	NA	NA
ELE_DENSITY:AVG_SHADE:AVG_DIST_TREES:RESERVEUmbabat	NA	NA	NA	NA
PRECIP:AVG_SHADE:AVG_DIST_TREES:RESERVEKapama	NA	NA	NA	NA
PRECIP:AVG_SHADE:AVG_DIST_TREES:RESERVEKlaserie	NA	NA	NA	NA
PRECIP:AVG_SHADE:AVG_DIST_TREES:RESERVEUmbabat	NA	NA	NA	NA
ELE_DENSITY:PRECIP:AVG_SHADE:AVG_DIST_TREES:RESERVEKapama	NA	NA	NA	NA
ELE_DENSITY:PRECIP:AVG_SHADE:AVG_DIST_TREES:RESERVEKlaserie	NA	NA	NA	NA
ELE_DENSITY:PRECIP:AVG_SHADE:AVG_DIST_TREES:RESERVEUmbabat	NA	NA	NA	NA

3.20. Impala Density Two Years Post-Recolonization

	estimate	std.error	t.value	p.value
(Intercept)	-0.226	1.257	-0.180	0.859
ELE_DENSITY	43.459	150.590	0.289	0.775
PRECIP	0.001	0.003	0.337	0.739
AVG_SHADE	0.421	0.663	0.634	0.532
AVG_DIST_TREES	-0.014	0.016	-0.878	0.388
RESERVEKapama	-0.160	0.921	-0.174	0.863
RESERVEKlaserie	NA	NA	NA	NA
RESERVEUmbabat	NA	NA	NA	NA
ELE_DENSITY:PRECIP	-0.126	0.311	-0.404	0.690
ELE_DENSITY:AVG_SHADE	-48.700	65.126	-0.748	0.462
PRECIP:AVG_SHADE	-0.001	0.001	-1.124	0.272
ELE_DENSITY:AVG_DIST_TREES	1.234	1.682	0.734	0.470
PRECIP:AVG_DIST_TREES	0.000	0.000	1.374	0.182
AVG_SHADE:AVG_DIST_TREES	NA	NA	NA	NA
ELE_DENSITY:RESERVEKapama	97.742	273.675	0.357	0.724
ELE_DENSITY:RESERVEKlaserie	NA	NA	NA	NA
ELE_DENSITY:RESERVEUmbabat	NA	NA	NA	NA
PRECIP:RESERVEKapama	0.001	0.003	0.352	0.728
PRECIP:RESERVEKlaserie	NA	NA	NA	NA
PRECIP:RESERVEUmbabat	NA	NA	NA	NA
AVG_SHADE:RESERVEKapama	NA	NA	NA	NA
AVG_SHADE:RESERVEKlaserie	NA	NA	NA	NA
AVG_SHADE:RESERVEUmbabat	NA	NA	NA	NA
AVG_DIST_TREES:RESERVEKapama	NA	NA	NA	NA
AVG_DIST_TREES:RESERVEKlaserie	NA	NA	NA	NA
AVG_DIST_TREES:RESERVEUmbabat	NA	NA	NA	NA
ELE_DENSITY:PRECIP:AVG_SHADE	0.157	0.133	1.184	0.248
ELE_DENSITY:PRECIP:AVG_DIST_TREES	-0.004	0.004	-1.169	0.253
ELE_DENSITY:AVG_SHADE:AVG_DIST_TREES	NA	NA	NA	NA
PRECIP:AVG_SHADE:AVG_DIST_TREES	NA	NA	NA	NA
ELE_DENSITY:PRECIP:RESERVEKapama	-0.406	0.895	-0.453	0.654
ELE_DENSITY:PRECIP:RESERVEKlaserie	NA	NA	NA	NA
ELE_DENSITY:PRECIP:RESERVEUmbabat	NA	NA	NA	NA
ELE_DENSITY:AVG_SHADE:RESERVEKapama	NA	NA	NA	NA
ELE_DENSITY:AVG_SHADE:RESERVEKlaserie	NA	NA	NA	NA
ELE_DENSITY:AVG_SHADE:RESERVEUmbabat	NA	NA	NA	NA
PRECIP:AVG_SHADE:RESERVEKapama	NA	NA	NA	NA
PRECIP:AVG_SHADE:RESERVEKlaserie	NA	NA	NA	NA
PRECIP:AVG_SHADE:RESERVEUmbabat	NA	NA	NA	NA
ELE_DENSITY:AVG_DIST_TREES:RESERVEKapama	NA	NA	NA	NA
ELE_DENSITY:AVG_DIST_TREES:RESERVEKlaserie	NA	NA	NA	NA
ELE_DENSITY:AVG_DIST_TREES:RESERVEUmbabat	NA	NA	NA	NA
PRECIP:AVG_DIST_TREES:RESERVEKapama	NA	NA	NA	NA
PRECIP:AVG_DIST_TREES:RESERVEKlaserie	NA	NA	NA	NA
PRECIP:AVG_DIST_TREES:RESERVEUmbabat	NA	NA	NA	NA
AVG_SHADE:AVG_DIST_TREES:RESERVEKapama	NA	NA	NA	NA
AVG_SHADE:AVG_DIST_TREES:RESERVEKlaserie	NA	NA	NA	NA
AVG_SHADE:AVG_DIST_TREES:RESERVEUmbabat	NA	NA	NA	NA
ELE_DENSITY:PRECIP:AVG_SHADE:AVG_DIST_TREES	NA	NA	NA	NA
ELE_DENSITY:PRECIP:AVG_SHADE:RESERVEKapama	NA	NA	NA	NA
ELE_DENSITY:PRECIP:AVG_SHADE:RESERVEKlaserie	NA	NA	NA	NA
ELE_DENSITY:PRECIP:AVG_SHADE:RESERVEUmbabat	NA	NA	NA	NA
ELE_DENSITY:PRECIP:AVG_DIST_TREES:RESERVEKapama	NA	NA	NA	NA
ELE_DENSITY:PRECIP:AVG_DIST_TREES:RESERVEKlaserie	NA	NA	NA	NA
ELE_DENSITY:PRECIP:AVG_DIST_TREES:RESERVEUmbabat	NA	NA	NA	NA
ELE_DENSITY:AVG_SHADE:AVG_DIST_TREES:RESERVEKapama	NA	NA	NA	NA
ELE_DENSITY:AVG_SHADE:AVG_DIST_TREES:RESERVEKlaserie	NA	NA	NA	NA
ELE_DENSITY:AVG_SHADE:AVG_DIST_TREES:RESERVEUmbabat	NA	NA	NA	NA
PRECIP:AVG_SHADE:AVG_DIST_TREES:RESERVEKapama	NA	NA	NA	NA
PRECIP:AVG_SHADE:AVG_DIST_TREES:RESERVEKlaserie	NA	NA	NA	NA
PRECIP:AVG_SHADE:AVG_DIST_TREES:RESERVEUmbabat	NA	NA	NA	NA
ELE_DENSITY:PRECIP:AVG_SHADE:AVG_DIST_TREES:RESERVEKapama	NA	NA	NA	NA
ELE_DENSITY:PRECIP:AVG_SHADE:AVG_DIST_TREES:RESERVEKlaserie	NA	NA	NA	NA
ELE_DENSITY:PRECIP:AVG_SHADE:AVG_DIST_TREES:RESERVEUmbabat	NA	NA	NA	NA

3.21. Kudu Density One Year Post-Recolonization

	estimate	std.error	t.value	p.value
(Intercept)	0.044	0.042	1.051	0.301
ELE_DENSITY	-3.667	5.136	-0.714	0.481
PRECIP	0.000	0.000	-0.666	0.511
AVG_SHADE	-0.036	0.024	-1.533	0.136
AVG_DIST_TREES	0.000	0.001	0.696	0.492
RESERVEKapama	0.037	0.024	1.559	0.129
RESERVEKlaserie	NA	NA	NA	NA
RESERVEUmbabat	NA	NA	NA	NA
ELE_DENSITY:PRECIP	0.004	0.011	0.309	0.760
ELE_DENSITY:AVG_SHADE	3.312	2.327	1.423	0.165
PRECIP:AVG_SHADE	0.000	0.000	1.150	0.259
ELE_DENSITY:AVG_DIST_TREES	-0.040	0.057	-0.700	0.489
PRECIP:AVG_DIST_TREES	0.000	0.000	-0.594	0.557
AVG_SHADE:AVG_DIST_TREES	NA	NA	NA	NA
ELE_DENSITY:RESERVEKapama	-9.066	5.943	-1.525	0.138
ELE_DENSITY:RESERVEKlaserie	NA	NA	NA	NA
ELE_DENSITY:RESERVEUmbabat	NA	NA	NA	NA
PRECIP:RESERVEKapama	0.000	0.000	-1.820	0.079
PRECIP:RESERVEKlaserie	NA	NA	NA	NA
PRECIP:RESERVEUmbabat	NA	NA	NA	NA
AVG_SHADE:RESERVEKapama	NA	NA	NA	NA
AVG_SHADE:RESERVEKlaserie	NA	NA	NA	NA
AVG_SHADE:RESERVEUmbabat	NA	NA	NA	NA
AVG_DIST_TREES:RESERVEKapama	NA	NA	NA	NA
AVG_DIST_TREES:RESERVEKlaserie	NA	NA	NA	NA
AVG_DIST_TREES:RESERVEUmbabat	NA	NA	NA	NA
ELE_DENSITY:PRECIP:AVG_SHADE	-0.005	0.005	-0.983	0.334
ELE_DENSITY:PRECIP:AVG_DIST_TREES	0.000	0.000	0.711	0.483
ELE_DENSITY:AVG_SHADE:AVG_DIST_TREES	NA	NA	NA	NA
PRECIP:AVG_SHADE:AVG_DIST_TREES	NA	NA	NA	NA
ELE_DENSITY:PRECIP:RESERVEKapama	0.022	0.012	1.750	0.090
ELE_DENSITY:PRECIP:RESERVEKlaserie	NA	NA	NA	NA
ELE_DENSITY:PRECIP:RESERVEUmbabat	NA	NA	NA	NA
ELE_DENSITY:AVG_SHADE:RESERVEKapama	NA	NA	NA	NA
ELE_DENSITY:AVG_SHADE:RESERVEKlaserie	NA	NA	NA	NA
ELE_DENSITY:AVG_SHADE:RESERVEUmbabat	NA	NA	NA	NA
PRECIP:AVG_SHADE:RESERVEKapama	NA	NA	NA	NA
PRECIP:AVG_SHADE:RESERVEKlaserie	NA	NA	NA	NA
PRECIP:AVG_SHADE:RESERVEUmbabat	NA	NA	NA	NA
ELE_DENSITY:AVG_DIST_TREES:RESERVEKapama	NA	NA	NA	NA
ELE_DENSITY:AVG_DIST_TREES:RESERVEKlaserie	NA	NA	NA	NA
ELE_DENSITY:AVG_DIST_TREES:RESERVEUmbabat	NA	NA	NA	NA
PRECIP:AVG_DIST_TREES:RESERVEKapama	NA	NA	NA	NA
PRECIP:AVG_DIST_TREES:RESERVEKlaserie	NA	NA	NA	NA
PRECIP:AVG_DIST_TREES:RESERVEUmbabat	NA	NA	NA	NA
AVG_SHADE:AVG_DIST_TREES:RESERVEKapama	NA	NA	NA	NA
AVG_SHADE:AVG_DIST_TREES:RESERVEKlaserie	NA	NA	NA	NA
AVG_SHADE:AVG_DIST_TREES:RESERVEUmbabat	NA	NA	NA	NA
ELE_DENSITY:PRECIP:AVG_SHADE:AVG_DIST_TREES	NA	NA	NA	NA
ELE_DENSITY:PRECIP:AVG_SHADE:RESERVEKapama	NA	NA	NA	NA
ELE_DENSITY:PRECIP:AVG_SHADE:RESERVEKlaserie	NA	NA	NA	NA
ELE_DENSITY:PRECIP:AVG_SHADE:RESERVEUmbabat	NA	NA	NA	NA
ELE_DENSITY:PRECIP:AVG_DIST_TREES:RESERVEKapama	NA	NA	NA	NA
ELE_DENSITY:PRECIP:AVG_DIST_TREES:RESERVEKlaserie	NA	NA	NA	NA
ELE_DENSITY:PRECIP:AVG_DIST_TREES:RESERVEUmbabat	NA	NA	NA	NA
ELE_DENSITY:AVG_SHADE:AVG_DIST_TREES:RESERVEKapama	NA	NA	NA	NA
ELE_DENSITY:AVG_SHADE:AVG_DIST_TREES:RESERVEKlaserie	NA	NA	NA	NA
ELE_DENSITY:AVG_SHADE:AVG_DIST_TREES:RESERVEUmbabat	NA	NA	NA	NA
PRECIP:AVG_SHADE:AVG_DIST_TREES:RESERVEKapama	NA	NA	NA	NA
PRECIP:AVG_SHADE:AVG_DIST_TREES:RESERVEKlaserie	NA	NA	NA	NA
PRECIP:AVG_SHADE:AVG_DIST_TREES:RESERVEUmbabat	NA	NA	NA	NA
ELE_DENSITY:PRECIP:AVG_SHADE:AVG_DIST_TREES:RESERVEKapama	NA	NA	NA	NA
ELE_DENSITY:PRECIP:AVG_SHADE:AVG_DIST_TREES:RESERVEKlaserie	NA	NA	NA	NA
ELE_DENSITY:PRECIP:AVG_SHADE:AVG_DIST_TREES:RESERVEUmbabat	NA	NA	NA	NA

3.22. Kudu Density Two Years Post-Recolonization

	estimate	std.error	t.value	p.value
(Intercept)	-2E-04	5E-02	-4E-03	1E+00
ELE_DENSITY	2E+00	6E+00	4E-01	7E-01
PRECIP	3E-05	1E-04	2E-01	8E-01
AVG_SHADE	-3E-02	3E-02	-1E+00	3E-01
AVG_DIST_TREES	1E-03	6E-04	2E+00	7E-02
RESERVEKapama	8E-03	4E-02	2E-01	8E-01
RESERVEKlaserie	NA	NA	NA	NA
RESERVEUmbabat	NA	NA	NA	NA
ELE_DENSITY:PRECIP	-8E-03	1E-02	-6E-01	5E-01
ELE_DENSITY:AVG_SHADE	2E+00	3E+00	6E-01	5E-01
PRECIP:AVG_SHADE	5E-05	6E-05	9E-01	4E-01
ELE_DENSITY:AVG_DIST_TREES	-1E-01	7E-02	-2E+00	7E-02
PRECIP:AVG_DIST_TREES	-3E-06	1E-06	-2E+00	7E-02
AVG_SHADE:AVG_DIST_TREES	NA	NA	NA	NA
ELE_DENSITY:RESERVEKapama	-5E+00	1E+01	-4E-01	7E-01
ELE_DENSITY:RESERVEKlaserie	NA	NA	NA	NA
ELE_DENSITY:RESERVEUmbabat	NA	NA	NA	NA
PRECIP:RESERVEKapama	-8E-05	1E-04	-6E-01	5E-01
PRECIP:RESERVEKlaserie	NA	NA	NA	NA
PRECIP:RESERVEUmbabat	NA	NA	NA	NA
AVG_SHADE:RESERVEKapama	NA	NA	NA	NA
AVG_SHADE:RESERVEKlaserie	NA	NA	NA	NA
AVG_SHADE:RESERVEUmbabat	NA	NA	NA	NA
AVG_DIST_TREES:RESERVEKapama	NA	NA	NA	NA
AVG_DIST_TREES:RESERVEKlaserie	NA	NA	NA	NA
AVG_DIST_TREES:RESERVEUmbabat	NA	NA	NA	NA
ELE_DENSITY:PRECIP:AVG_SHADE	-3E-03	5E-03	-5E-01	6E-01
ELE_DENSITY:PRECIP:AVG_DIST_TREES	3E-04	1E-04	2E+00	5E-02
ELE_DENSITY:AVG_SHADE:AVG_DIST_TREES	NA	NA	NA	NA
PRECIP:AVG_SHADE:AVG_DIST_TREES	NA	NA	NA	NA
ELE_DENSITY:PRECIP:RESERVEKapama	3E-02	4E-02	7E-01	5E-01
ELE_DENSITY:PRECIP:RESERVEKlaserie	NA	NA	NA	NA
ELE_DENSITY:PRECIP:RESERVEUmbabat	NA	NA	NA	NA
ELE_DENSITY:AVG_SHADE:RESERVEKapama	NA	NA	NA	NA
ELE_DENSITY:AVG_SHADE:RESERVEKlaserie	NA	NA	NA	NA
ELE_DENSITY:AVG_SHADE:RESERVEUmbabat	NA	NA	NA	NA
PRECIP:AVG_SHADE:RESERVEKapama	NA	NA	NA	NA
PRECIP:AVG_SHADE:RESERVEKlaserie	NA	NA	NA	NA
PRECIP:AVG_SHADE:RESERVEUmbabat	NA	NA	NA	NA
ELE_DENSITY:AVG_DIST_TREES:RESERVEKapama	NA	NA	NA	NA
ELE_DENSITY:AVG_DIST_TREES:RESERVEKlaserie	NA	NA	NA	NA
ELE_DENSITY:AVG_DIST_TREES:RESERVEUmbabat	NA	NA	NA	NA
PRECIP:AVG_DIST_TREES:RESERVEKapama	NA	NA	NA	NA
PRECIP:AVG_DIST_TREES:RESERVEKlaserie	NA	NA	NA	NA
PRECIP:AVG_DIST_TREES:RESERVEUmbabat	NA	NA	NA	NA
AVG_SHADE:AVG_DIST_TREES:RESERVEKapama	NA	NA	NA	NA
AVG_SHADE:AVG_DIST_TREES:RESERVEKlaserie	NA	NA	NA	NA
AVG_SHADE:AVG_DIST_TREES:RESERVEUmbabat	NA	NA	NA	NA
ELE_DENSITY:PRECIP:AVG_SHADE:AVG_DIST_TREES	NA	NA	NA	NA
ELE_DENSITY:PRECIP:AVG_SHADE:RESERVEKapama	NA	NA	NA	NA
ELE_DENSITY:PRECIP:AVG_SHADE:RESERVEKlaserie	NA	NA	NA	NA
ELE_DENSITY:PRECIP:AVG_SHADE:RESERVEUmbabat	NA	NA	NA	NA
ELE_DENSITY:PRECIP:AVG_DIST_TREES:RESERVEKapama	NA	NA	NA	NA
ELE_DENSITY:PRECIP:AVG_DIST_TREES:RESERVEKlaserie	NA	NA	NA	NA
ELE_DENSITY:PRECIP:AVG_DIST_TREES:RESERVEUmbabat	NA	NA	NA	NA
ELE_DENSITY:AVG_SHADE:AVG_DIST_TREES:RESERVEKapama	NA	NA	NA	NA
ELE_DENSITY:AVG_SHADE:AVG_DIST_TREES:RESERVEKlaserie	NA	NA	NA	NA
ELE_DENSITY:AVG_SHADE:AVG_DIST_TREES:RESERVEUmbabat	NA	NA	NA	NA
PRECIP:AVG_SHADE:AVG_DIST_TREES:RESERVEKapama	NA	NA	NA	NA
PRECIP:AVG_SHADE:AVG_DIST_TREES:RESERVEKlaserie	NA	NA	NA	NA
PRECIP:AVG_SHADE:AVG_DIST_TREES:RESERVEUmbabat	NA	NA	NA	NA
ELE_DENSITY:PRECIP:AVG_SHADE:AVG_DIST_TREES:RESERVEKapama	NA	NA	NA	NA
ELE_DENSITY:PRECIP:AVG_SHADE:AVG_DIST_TREES:RESERVEKlaserie	NA	NA	NA	NA
ELE_DENSITY:PRECIP:AVG_SHADE:AVG_DIST_TREES:RESERVEUmbabat	NA	NA	NA	NA