

EXAMINING FACTORS INFLUENCING MAMMAL OCCURRENCE AND ASSEMBLY

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ABSTRACT

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In this dissertation, I examined the role of communication, group size, phylogeny, and illegal human harvest (i.e., poaching) in structuring mammalian occurrence, activity, social behavior, and assembly. This research is divided among four dissertation chapters, each representing an independent manuscript, two of which are published. In chapter one, I explored the multiple modalities by which giraffe (*Giraffa camelopardalis*) communicate. Via an extensive review, I found just 21 studies, published between 1958 and 2018, referencing giraffe communication across visual, olfactory, and auditory dimensions. I found that incorrect generalizations about giraffe communication (such as the belief that this species was mute) were simply a byproduct of inadequate research efforts. In reality, giraffes regularly produce infrasonic sounds, hisses, and low humming vocalizations. Additionally, giraffes have strong visual and olfactory capabilities that they depend on for communication. From this research, I found that giraffes communicate via multimodal signals, but more research is needed to examine the intent and context of communication.

In chapter two, I examined the ways researchers estimate ungulate group sizes. Spatial extents (i.e., nearest neighbor distances) over which ungulate group sizes were defined ranged between 1.4 m to 1000 m whereas temporal extents ranged between three minutes to 24 hours. The variability in group size definitions that I observed complicates efforts to not only compare and replicate studies, but also to evaluate underlying theories of group living. In chapter three, I examined the prevalence and spatial distribution of giraffes with snaring injuries in Murchison

Falls National Park (MFNP), Uganda. Via photographic spatial encounter surveys and using coat patterns to identify animals, I observed a subadult/adult population of 1,306 and estimated 1,892 (± 78) using a spatial capture-recapture model. Model predictions showed that only 1.3% of the population had a snaring injury, and these individuals were concentrated on the western end of the park close to the River Nile shores. Individual giraffes with highest movement rates in the landscape had higher chances of being snared. I contend that even when giraffes are not targeted by poachers, they can still experience important individual-level effects from wire snares.

Finally, in chapter four, I examined the role of body mass and phylogeny in predicting mammal activity in MFNP. My results indicated that phylogeny is a statistically-stronger predictor of mammal activity levels (time spent active in 24-hours) than body mass. These results suggest that variation in activity among co-occurring mammals is structured with respect to phylogeny. Thus, phylogeny plays a critical role in mammal community assembly. Overall, my research emphasizes a broad scale and multidimensional evaluation of mammal occurrence and assembly.

To Jeremiah Bogezi, Jason Zinda, and my future children.
I hope you will be inspired!

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PREFACE

Two of the chapters of this dissertation have been published in peer-reviewed journals with co-authors. Due to copyright, the published chapters could not be reprinted in this dissertation. I briefly summarize each and provide a link to the online article.

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INTRODUCTION

The evolution of animals is believed to have started approximately 600 million years ago leading to numerous species occupying different biomes around the world (Nielsen, 2019). Within these biomes, animal life history characteristics along with their habitat interactions shape occurrence and assembly patterns (Breed & Sanchez, 2010). Since the quaternary period (approximately 2.6 million years ago), humans (*Homo sapiens*) have had disproportionate influence on animal communities (Sandom et al., 2014). For example, in the late Pleistocene and early Holocene, human impacts have been linked to extinction of numerous large vertebrate species (Barnosky et al., 2004). Thus, factors driving patterns of animal occurrence and assembly are evolutionary, ecological, and anthropogenic. In this dissertation, I explored the influence of these factors on mammal occurrence and assembly via examining the role of communication (chapter one), sociality (chapter two), poaching (chapter three), and phylogeny (chapter four).

Inter- and intra-species communication is integral to expression of behavior and mediating animal assembly (Kaplan, 2014). Animals communicate via several modalities, including production of vocal, olfactory, and visual signals as well as electrical perception (Laidre & Johnstone, 2013; Kaplan, 2014; Fischer et al., 2017). Animal communication research is facilitated by advances in technology which have led to manufacture of innovative equipment useful for recording communication signals (Kaplan, 2014). To this end, numerous studies have examined communication pathways among birds (Wheatcroft & Price, 2003), primates (Fischer et al., 2017), elephants (Soltis et al., 2005), dolphins (Tyack, 2000), and other animals. However, fundamental communication knowledge is still lacking for many species. One of those is the giraffe (*Giraffa camelopardalis*) whose communication abilities have largely been a mystery among both researchers and society. In chapter one of this dissertation, I explored the multiple

modalities by which giraffes communicate. I synthesized information from published studies describing the anatomy of sensory organs, communication signals (such as vocal and olfactory), as well as patterns of social behavior. Finally, I described the role of communication in giraffe ecology and highlighted avenues for future research.

Social animal species evolved to live in groups mediated by complex communication systems (Krause & Ruxton, 2002). In this regard, forage distribution, predation risk, mating strategies, and habitat characteristics determine the mode of sociality (Jarman, 1974). For example, species living under high risk of predation may form and maintain strong social bonds (Dunbar & Schultz, 2010). Whereas increasing competition for forage among such grouping individuals may result in group disintegration despite the predation risk (Body et al., 2015). Therefore, group sizes reflect tradeoffs between costs and benefits of sociality as animals strive to maximize their fitness (Krause & Ruxton, 2002). Group size is a social trait commonly used to evaluate animal sociality and associated tradeoffs. Within this context, several theories and hypotheses have been formulated to explain animal sociality. For example, among others, the selfish herd hypothesis (where selfish predator avoidance leads to individual aggregation; Caro, 2005), the many eyes effect (useful for the detection of predators; Caro, 2005), and the social brain hypothesis (linked to positive associations between group cohesiveness and the development of cognitive abilities; Clutton-Brock & Coulson, 2002). Despite formulation of theories and hypotheses explaining group living, there has not been a consistent group definition across many species, study sites, and study contexts. This has been largely attributable to lack of foundational empirical, ecological, as well as evolutionary frameworks examining animal group sizes across space and time. In chapter two of this dissertation, I examined the extent of variability in estimation of ungulate group sizes across ecological studies. To achieve this

objective, I examined group size definitions of 61 species from studies examining ungulate sociality conducted between 1962 and 2018. From this synthesis, I formulated a novel framework for ungulate group size estimation.

While the first two chapters examined behavioral factors influencing animal occurrence and assembly, in the third chapter, I explored the role of poaching. The global increase in human population has continually led to expansion of human ecological footprint (Venter et al., 2016). Thus, activities such as illegal harvest of wildlife (i.e., poaching) have increased disproportionately in many areas (Ripple et al., 2016). Humans use a variety of tools when poaching including firearms, snares (made from either wire or sisal), spears, wheel traps, and others (Gray et al., 2018). Unsustainable poaching has caused population declines among many animal species, driving some to the brink of local extinction (Ripple et al., 2016). In addition, studies found that poaching altered animal behavior, genetic structure, as well as ecosystem function (Ripple et al., 2014; Carter et al., 2017). Poaching studies however, tend to focus on assessing the consequences for species specifically targeted by poachers. However, trapping methods (such as snares) are often indiscriminate and affect a broad range of non-target species when incidentally caught (Noss, 1998). In chapter three of this dissertation, I examined the prevalence and spatial configuration of giraffes with snaring injuries in Murchison Falls National Park, Uganda. While poaching has been consistently listed among the threats to giraffe conservation, examination of poaching impacts within this species is rare. I discussed the individual-level effects of snaring injuries and their implications for giraffe population persistence.

In the final chapter, I examined the role of phylogeny and species body mass in structuring activity within mammal communities. Activity among animals has been consistently

defined in terms of the times of day in which animals maintain active versus passive behavioral states (Halle & Stenseth, 2000). The levels to which animals are engaged in passive or active behaviors depends upon their metabolic needs, competition, energetic constraints, predation risk, human activity, and other factors (Jarman, 1974). Furthermore, metabolic needs and energetic constraints inherent to these behavioral decisions depend, at least in part, on species body mass (Brown et al., 2004). Within animal communities, species exhibit variability in energy requirements and acquisition techniques (Smith & Lyons, 2011), and therefore have different activity levels (i.e., time spent active in a day; Rowcliffe et al., 2014) and schedules. This variability in animal activity is shaped by evolution to enable species coexistence (Baker et al., 2015). In chapter four of this dissertation, I examined the relative role of phylogeny and body mass in predicting mammal activity. I also investigated pairwise overlap in activity schedules of phylogenetically-close species. I conclude the dissertation with a synthesis of the work and recommendations for future research.

CHAPTER 1: THE IMPORTANCE OF COMMUNICATION IN GIRAFFE ECOLOGY AND BEHAVIOR

I reviewed published studies that examined giraffe communication across visual, olfactory, and auditory dimensions. I synthesized information mainly from studies examining the anatomy of sensory organs to infer giraffe communication abilities. I found that giraffes communicate via multimodal signals including vocalizations (infrasonic, hisses, and hums), visual, and olfactory. I recommended future studies to examine the intent and propagation of these signals to further demystify giraffe communication. For a full text of this work, go to:

<https://doi.org/10.1111/jzo.12604>

CHAPTER 2: CONSEQUENCES OF VARYING UNGULATE GROUP SIZE ESTIMATION FOR ECOLOGICAL INFERENCE

I explored the consequences of varying ungulate group size definitions for ecological inference. I found high variability in the ways researchers examine and define group sizes within and between species. In addition, group size definitions were often subjective with no supporting empirical, ecological, or evolutionary foundations. This variation complicates efforts to replicate studies and to evaluate theory of group living. I recommended the formulation of foundational empirical rationale for defining animal groups. For a full text of this work, go to:

<https://doi.org/10.1002/ece3.6463>

CHAPTER 3: IMPLICATIONS OF INCIDENTAL POACHING FOR GIRAFFE POPULATION PERSISTENCE

Abstract

Illegal harvesting (i.e., poaching) is a geographically widespread threat to animal populations. Correspondingly, many tools are used to poach around the world, with wire snares common in the Global South. Wire snares are indiscriminate with respect to species, age, and sex of individual animals that they capture. When caught, very large mammals can break the wire snare away from its anchor (typically tree trunks). Such incidents leave these individual animals with severe injuries. The prevalence of snaring injuries as well as the ecological and conservation implications of such patterns have not been widely investigated. I investigated the prevalence and spatial variation of giraffe (*Giraffa camelopardalis*) snaring injuries in Murchison Falls National Park, Uganda, a system which experiences high rates of wire snaring. I conducted photographic spatial encounter surveys along five fixed road transects to detect individual giraffes with snaring injuries. I identified individual giraffes based on autonomous image processing of pelage patterns. I then fit a spatial capture-recapture (SCR) model to the encounter history data to quantify population-level parameter estimates and predict the spatial configuration of injured giraffes. I detected 1,306 individual adult and subadult giraffes from the spatial encounter surveys and predicted 1,892 (± 78) via the SCR model. I encountered 24 giraffes with detectable snaring injuries, corresponding to a population-level snaring probability of 1.3%. Snaring risk was positively related to individual movement rates. I contend that giraffes experience important individual-level effects from wire snares. Severed and broken limbs not only reduce mating and foraging efficiency, but can lead to secondary infections and increased

mortality. These impacts have the potential to negatively affect population growth rates if a higher proportion of individuals is affected.

Introduction

The illegal harvest of wild animals, commonly referred to as poaching, presents an important threat to the conservation of a broad range of species around the world (Madden, 2004; König et al., 2020). In this regard, poaching is a proximate factor associated with population declines of approximately 27% of the world's 1,169 threatened species listed by the International Union for Conservation of Nature (Ripple et al., 2016). Broadly, three forms of poaching have been identified including trophy (where animal parts are harvested as possessions), medicative (where animal parts are taken for curative uses), and consumptive (where animal parts are harvested for human nourishment; Muth & Bowe, 1998; Montgomery, 2020). A sub-form of consumptive poaching is subsistence poaching where animals are consumed directly within poacher's families (Gray et al., 2017; Montgomery, 2020). Subsistence poaching occurs around the world, but is particularly common in the Global South (Challender & MacMillan, 2014; Hauenstein et al., 2019; Duporge et al., 2020).

In the Global South, subsistence poachers commonly deploy snares to trap animals (Gray et al., 2018; Mudumba et al., 2020). Snares can be made from a variety of locally-available materials including sisal rope and wire (Mudumba et al., 2020). To maximize their yield, poachers tend to place snares at high densities in habitats used by target species (Gray et al., 2017). When placed in the landscape, wire snares are indiscriminate with respect to species, age, and sex of animals that they capture (Noss, 1998; Gray et al., 2018). In this regard, wire snares are capable of capturing larger species such as ungulates which are often a target for poachers (Fa & Brown, 2009). With one end anchored to a tree, a wire snare trap consists of a noose of a

wide diameter, placed at a height sufficient to capture the target animal (Gray et al., 2018; Mudumba et al., 2020). The noose tightens around limbs, neck, or torso when the animal becomes entangled in the trap. Many trapped animals die without being recovered where they decay or are consumed by scavengers (Noss, 1998). Some very large mammal species are able to break the wire snare from its anchor. In the process however, these animals typically sustain injuries including broken or severed body parts (Noss, 1998).

Animals subjected to poaching pressure can experience both behavioral and ecological impacts that may scale from individuals to populations (Ripple et al., 2014; Carter et al., 2017). Behavioral consequences of poaching include destabilization of social organization (including mate selection and dominance patterns), increased nocturnality, divergence of migration patterns, and changes in habitat selection (Wielgus & Bunnell, 1994; Wielgus et al., 2001; Cappa et al., 2017). Ecological effects include population declines with subsequent impacts on ecosystem function (Milner-Gulland et al., 2003; Challender & MacMillan, 2014; Ripple et al., 2016; Schlossberg et al., 2018; Loveridge et al., 2020). Given that large mammals are comparatively long-lived, wide-ranging, occur at low densities, and have age-dependent survival and reproduction rates, their populations are at higher likelihood of being destabilized by poaching impacts (Creel & Creel, 2002; Eberhardt, 2002; Packer et al., 2005). Recent research has tended to focus on spatiotemporal trends (Critchlow et al., 2015; Duporge et al., 2020) and ecological effects of poaching on large mammals (Poulsen et al., 2017; Loveridge et al., 2020). Additional research is required to examine prevalence and spatial configuration of incidental poaching on non-target large mammals, especially among species of conservation concern.

Given their large size and strength, giraffe (*Giraffa camelopardalis*) frequently break free from the wire snares that entrap them. In the process, giraffes typically sustain injuries including

severed or fractured limbs that can lead to secondary infections (Francesconi & Lupi, 2012). Giraffes are presently considered vulnerable by the International Union for the Conservation of Nature (IUCN; Muller et al., 2018). In that regard, poaching has been suggested to be an important factor limiting giraffe population growth (Strauss et al., 2015; Ripple et al., 2015; Fennessy et al., 2018) but the effects of poaching at the individual- and population-level have not been widely described. Therefore, giraffes provide an important case study to examine prevalence and spatial distribution of incidental snare poaching on a non-target large mammal species of conservation concern. Herein, I quantified the proportion of the Rothschild's giraffe (*G. c. rothschildi*) population of Murchison Falls National Park (MFNP), Uganda with snaring injuries. I examined the spatial configuration of snared individuals as it relates to overall giraffe density. I also evaluated age- and sex-specific effects of snaring injuries on giraffe movement dynamics. I discuss the implications of this research for giraffe population persistence.

Methods

Study area

I conducted this study in the northern section of Murchison Falls National Park (MFNP; Figure 3.1) associated with the core distribution of giraffes in this landscape. Located in northwestern Uganda, MFNP is the largest protected area in the country covering approximately 3,898 km². The park is divided into northern and southern sections by the Victoria Nile river which flows 115 km from east to west. Additionally, the Albert Nile river borders the park on the west, restricting giraffe movements on this edge of the park. Vegetation of the northern section of MFNP includes open grasslands, dense woodlands, and thickets. The park has a hot and dry tropical climate characterized by two distinct weather seasons. The wet season lasts from April

to May and then again from August to October while the dry season occurs from December to February and June to September.

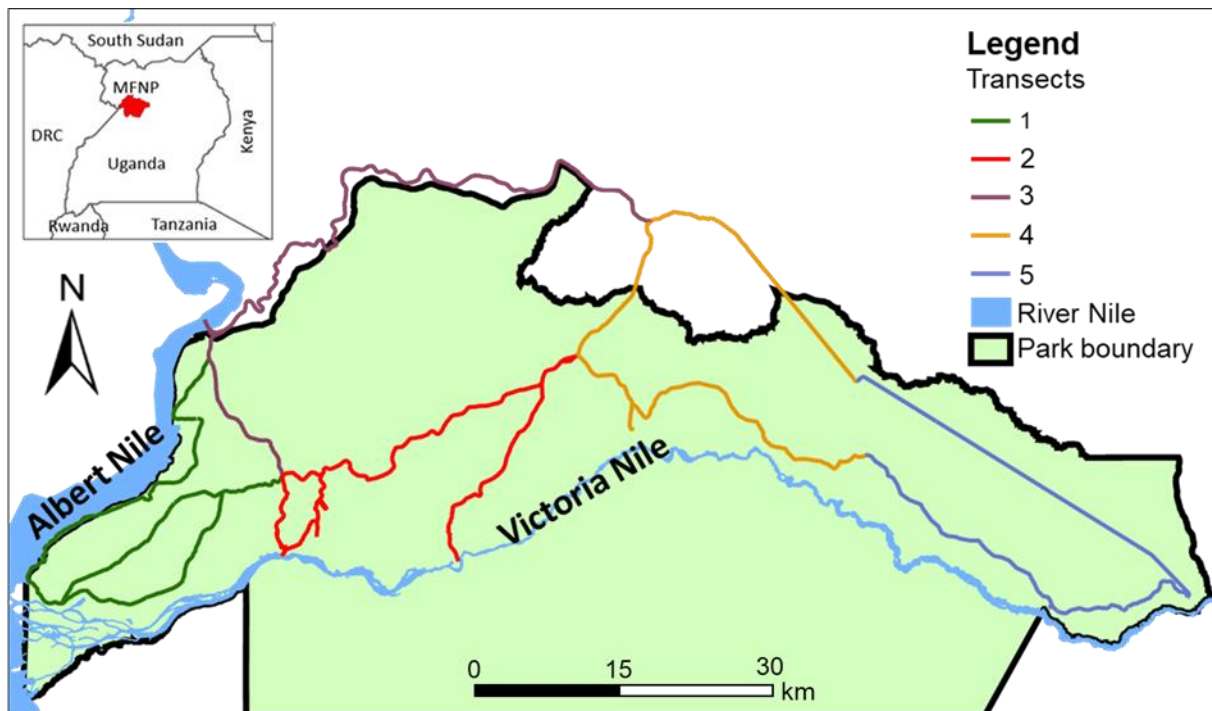


Figure 3.1. The five road transects used to survey Rothschild's giraffes (*Giraffa camelopardalis rothschildi*) in the northern section of Murchison Falls National Park, Uganda between June and August 2019. The inset features the location of MFNP in Uganda

Poaching in MFNP

Murchison Falls National Park experienced high levels of poaching as a byproduct of political instability in the 1970s and 80s, during which animal populations were heavily decimated (Douglas-Hamilton et al., 1980; Lamprey & Michelmore, 1995). Wire snare poaching remains at high levels to date, with poachers from adjacent villages commonly accessing MFNP via the Albert Nile and Victoria Nile waterways (Mudumba et al., 2020; Figure 3.1). Though the primary targets of poachers are typically antelopes, such as Uganda kob (*Kobus kob*) and

hartebeest (*Alcelaphus buselaphus*) (Mudumba et al., 2020), non-target species such as giraffes are also often entrapped.

I base the notion that giraffes are not targeted by subsistence poachers using wire snares in MFNP on three lines of reasoning. First, poachers typically set snare traps to capture target animal species around the neck (Noss, 1998; Gray et al., 2017). Research in MFNP has showed that wire snares are placed with the lower end at an average height of 0.42 m (range 0.00 m – 0.96 m) from the ground (Mudumba et al., 2020). Within this height range, snare traps are optimized to facilitate entrapment of target species (with shoulder heights ~1 m; Kingdon & Hoffmann, 2013) around the neck. In contrast, giraffes have a higher shoulder height (i.e., > 4 m; Kingdon & Hoffmann, 2013). Therefore, at snare trap heights <1 m, giraffes are essentially only trapped around the legs, where they often break free with injuries. In landscapes where giraffes are targeted by poachers, snares are set higher in the trees to trap giraffes around their necks (Strauss et al., 2015). Second, within the human communities living adjacent to MFNP, there is no evidence of local consumption of giraffe meat (Mudumba, 2019). Third, there is no evidence of the use of giraffe body parts in cultural practices in Uganda, as is the case in other areas in Africa (Dunn et al., 2021). Additionally, there is currently no evidence for giraffe parts sourced from Uganda for international trade (Harrison et al., 2015). Thus, by this logic, I assert that giraffes are incidentally caught in wire snares in MFNP.

Giraffe surveys

I conducted photographic spatial encounter surveys along five fixed routes between June and August 2019 (Figure 3.1). The five transects averaged 73.1 km $\pm$ 3.3 km in length and covered all representative habitat types in MFNP. I surveyed each transect 10 times to accumulate capture histories of giraffes among replicate surveys. I randomized start day and

direction travelled per transect for each replicate survey. With two observers positioned in the vehicle, we scanned both sides of each road transect within 200 m while driving at a consistent speed of 20 km/hr. Given the low speed, large body size of giraffes, and open vegetation characteristic of this landscape, giraffes were easily detectable within the 200 m of transect (*sensu* Muneza et al., 2017). I took georeferenced digital images of the right side of each detected giraffe using a CANON EOS REBEL T5 camera fitted with Sigma 150-600 mm Telephoto zoom lens or NIKON D5300 camera fitted with AF-P DX NIKKOR 70-300 mm Telephoto Zoom lens. I also recorded age (juvenile, subadult, or adult), sex, group size, and presence and location of snaring injuries for each detected individual. I sexed and separated age classes among individuals based on physical characteristics including ossicone size, pelage color, and genitalia. Adult bulls have two or three prominent ossicones covered with less hair, whereas females and young have smaller ossicones covered with thicker tufts of hair (Ciofolo & Pendu, 2013). I also used blotch darkening to identify older bulls (Berry, 1973; Estes, 1991).

I obtained each image at a right angle to the animal, following requirements for post-survey processing (see Muneza et al., 2017). I created a database of all images and discarded those taken at acute angles as well as those in which obstructions (i.e., vegetation or other giraffes) covered the area of interest on the animal. I first pre-processed images by cropping out undesired areas to retain only the extent of the giraffe's pelage pattern. I then uploaded cropped images to Wild-ID for processing. Wild-ID is a software that employs the Scale Invariant Feature Transform (SIFT; Lowe, 2004) algorithm to identify, extract, and match distinctive features in giraffe pelage patterns invariant to image scale, orientation, perspective, local distortion, and brightness (Lowe, 2004; Bolger et al., 2012). After pattern extraction and matching, Wild-ID ranks images based on pattern similarity (Bolger et al., 2012). I matched each

focal image with an identical one from five top ranked candidates after careful visual inspection (Bolger et al., 2012). If none of the five top ranked individuals matched the focal image, I recorded the focal image as a distinct individual.

Spatial capture-recapture modelling

I estimated the prevalence and spatial configuration of incidental poaching of giraffes at the population level using spatial capture-recapture (SCR) modelling for search-encounter designs (Efford, 2011; Royle et al., 2011, 2014). In the SCR framework, a spatial point process model of abundance and a spatial model of the detection process (observation model) are simultaneously fitted to individual encounter history data (Royle et al., 2014). For the abundance model, I derived estimates from a distribution of individual activity centers, $\mathbf{s}_i$, within the state space, S . I described the S as a discrete spatial unit where giraffes were detected. I assumed the activity centers to be uniformly distributed within the state space, $\mathbf{s}_i \sim \text{Uniform}[S]$. I restricted the state space to areas of suitable habitat for giraffes, to ensure accurate abundance and density estimates. As such, I clipped out areas of open water (the Albert- and Victoria Nile rivers, see Figure 3.1), human settlements, and agricultural lands adjacent to some sections of the northern boundary of the park. Given these restrictions, I expected zero probability of giraffe occurrence beyond the state space and created no buffer zone. I divided the state space into discrete 1 km x 1 km grid cells and considered the intersection between the grid cells and the transects as traps where individuals were detected (cf. Muneza et al., 2017).

The observation model involved estimating the probability or rate ($\lambda[\mathbf{x}, \mathbf{s}]$) of detecting an individual as a function of distance ($d[\mathbf{x}, \mathbf{s}]$) between a grid cell (i.e., trap), $\mathbf{x}_j$, and the individual's latent activity center, $\mathbf{s}_i$.

I described the detection rate using the half normal encounter probability model:

$$\lambda_{ij}[\mathbf{x}_j, \mathbf{s}_i] = \lambda_{0ij} \exp\left(-\frac{\|\mathbf{x}_j - \mathbf{s}_i\|^2}{2\sigma_i^2}\right)$$

where λ_{0ij} is the baseline encounter rate of detecting an individual at its activity center (i.e. $\mathbf{x}=\mathbf{s}$); and σ_i (the scale parameter) controls the rate of decline in individual detectability as the distance between $\mathbf{x}$ and $\mathbf{s}$ increases. Both the baseline encounter rate λ_{0ij} and the scale parameter σ_i , were allowed to vary according to individual attributes including 1) sex, with female as the reference category; 2) age class, with adult as the reference category; 3) an interaction of sex $\times$ age class; and 4) the presence/absence of a snaring injury. I estimated these relationships by specifying linear models on the log scale for each parameter, $\log(\lambda_{0ij}) = \mathbf{X}_i\boldsymbol{\alpha}$ and $\log(\sigma_i) = \mathbf{X}_i\boldsymbol{\delta}$, where $\mathbf{X}_i$ is the design matrix of individual attributes and the parameters to estimate are $\boldsymbol{\alpha}$ and $\boldsymbol{\delta}$. In addition to the individual attributes, I included an offset term on the encounter rate to adjust for total hours (i.e., effort) spent surveying grid cell j . I eliminated calves from the analysis as their encounters are dependent on those of their mothers (*sensu* Muneza et al., 2017), thus violating the assumption of independence among individual detections (Royle et al., 2014).

Following standard SCR models, I determined N as the number of $\mathbf{s}$ within S . To estimate N , I augmented the dataset (n observed individuals) with a large number of all zero encounter histories ($M-n$) and modeled the augmented dataset as a zero-inflated version of the complete-data model using a zero-inflation parameter (Royle et al., 2007). I set M as the super population from which N is drawn (i.e., $M > N$), where some of the all-zero encounter histories do not correspond to actual individuals within N (Royle et al., 2007, 2011). I assigned each individual in the augmented dataset a partially latent population membership indicator z_i , where $z_i = 1$ corresponded to true members of the population and $z_i = 0$ otherwise. Accordingly, $z_i = 1$ was

known for all n observed individuals and unknown ($z_i = \text{NA}$) for the $M-n$ individuals. I treated demographic attributes (sex, age, presence of snaring injury) as partially latent variables that were known for most observed individuals and unknown for the $M-n$ unobserved individuals. The binary individual attributes were all considered Bernoulli random variables with a corresponding probability, including that for population membership (ψ) and the other attributes (ψ_{male} , ψ_{subadult} , ψ_{snare}). I derived N from $\psi \times M$ and density, D , from dividing N by the area of S .

I fit the SCR model using a Bayesian framework and Markov Chain Monte Carlo simulations in the JAGS (Plummer, 2003) language implemented in R (R Core Team, 2020) via the package JAGSUI (Kellner, 2019). I ran three chains of 2,500 iterations each, following an adaptation period of 500. I used vague priors for all covariates and checked for model convergence using trace plots and R-hat statistics. R-hat values for all parameters were <1.1 , indicating model convergence (Gelman & Hill, 2007).

Results

Across the replicate photographic spatial encounter surveys, I retained and cropped a total of 5,444 images to facilitate individual animal identification in Wild-ID. Via this processing in Wild-ID, I detected and generated spatial encounter histories of 1,402 individual giraffes. Among the 1,402 individuals detected, there were 729 females and 671 males. I could not identify sex for 2 juvenile giraffes. Additionally, most giraffes in this population were adults ($n = 897$), followed by subadults ($n = 409$), and then juveniles ($n = 96$). During the surveys, I encountered 24 individuals with a snaring injury (Figure 3.2). The snared individuals included one juvenile male, 12 adult males, one adult female, eight subadult males, and two subadult females.

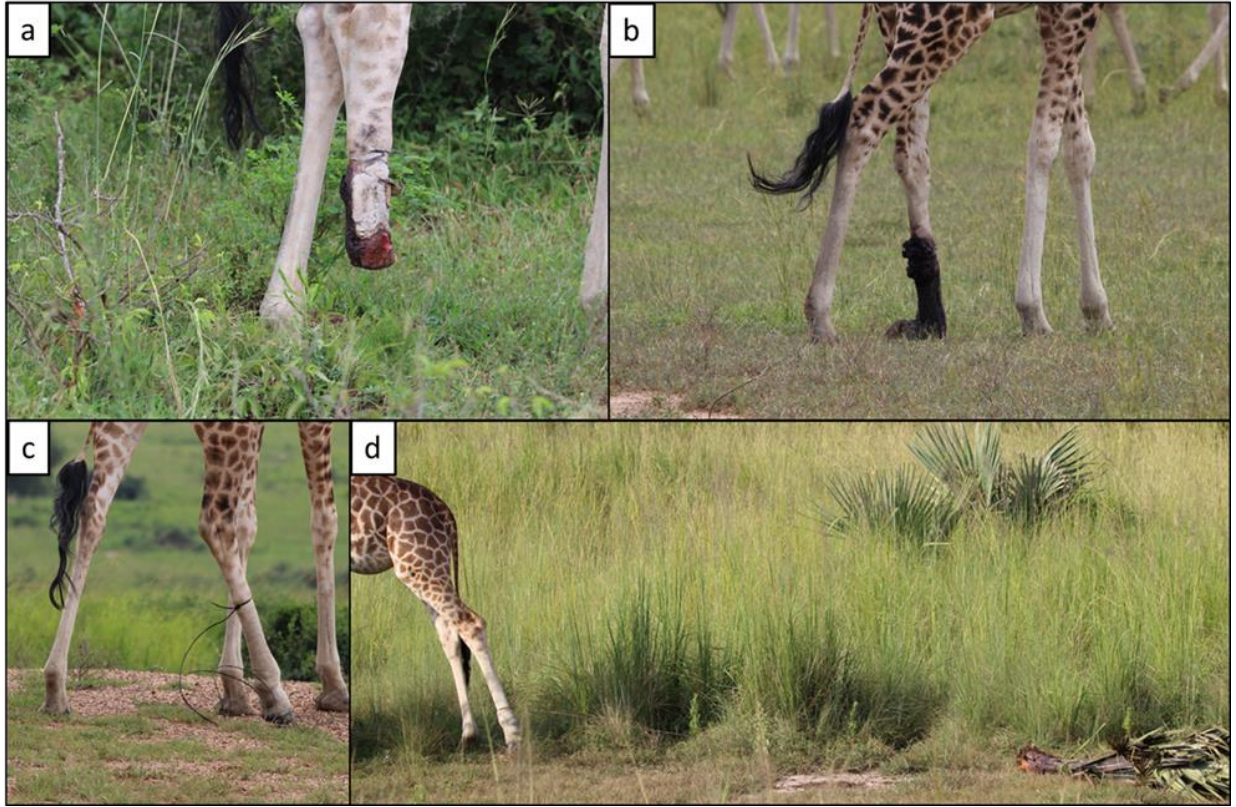


Figure 3.2. Wire snares commonly catch giraffes (*Giraffa camelopardalis rothschildi*) by their legs in Murchison Falls National Park, Uganda. As they fight to break free, individuals may lose the lower part of their leg (a), have their leg disfigured (b), break the wire snare off its anchor (c), or uproot the anchor with the wire (d). Photo credits: Herbert Kasozi

The SCR model estimated a mean adult/subadult giraffe population (N) of 1,892 individuals (95% CI: 1812, 1966), and a density (D) of 1.12 (95% CI: 1.08, 1.17) individuals/km² (Table 1). The estimated giraffe population had a lower proportion of males ($\psi_{\text{males}} = 0.45$ [95% CI: 0.42, 0.48]) compared to females, and subadults ($\psi_{\text{subadult}} = 0.35$ [95% CI: 0.32, 0.38]) compared to adults. Both giraffe sex and age had no strong effects on individual encounter rates. Adult males had higher movement rates ($\delta_1 = 0.09$ [0.01, 0.16]) than females. Whereas subadults moved less than adults ($\delta_2 = -0.14$ [-0.24, -0.04]) for both sexes. A relatively

low proportion of individuals in this giraffe population had a snaring injury ($\psi_{\text{snare}} = 0.013$ [95% CI: 0.008, 0.019]; Table 1). Snaring probability was positively associated with both individual movement rate ($\delta_4 = 0.19$ [0.02, 0.39]) and encounter rate ($\alpha_4 = 0.44$ [0.11, 0.77]; Table 1). Spatial predictions of realized density from the model depicted a higher probability of observing individuals with a snaring injury on the western side of the park, corresponding to areas of high giraffe density between the Albert and Victoria Nile rivers (Figure 3.3).

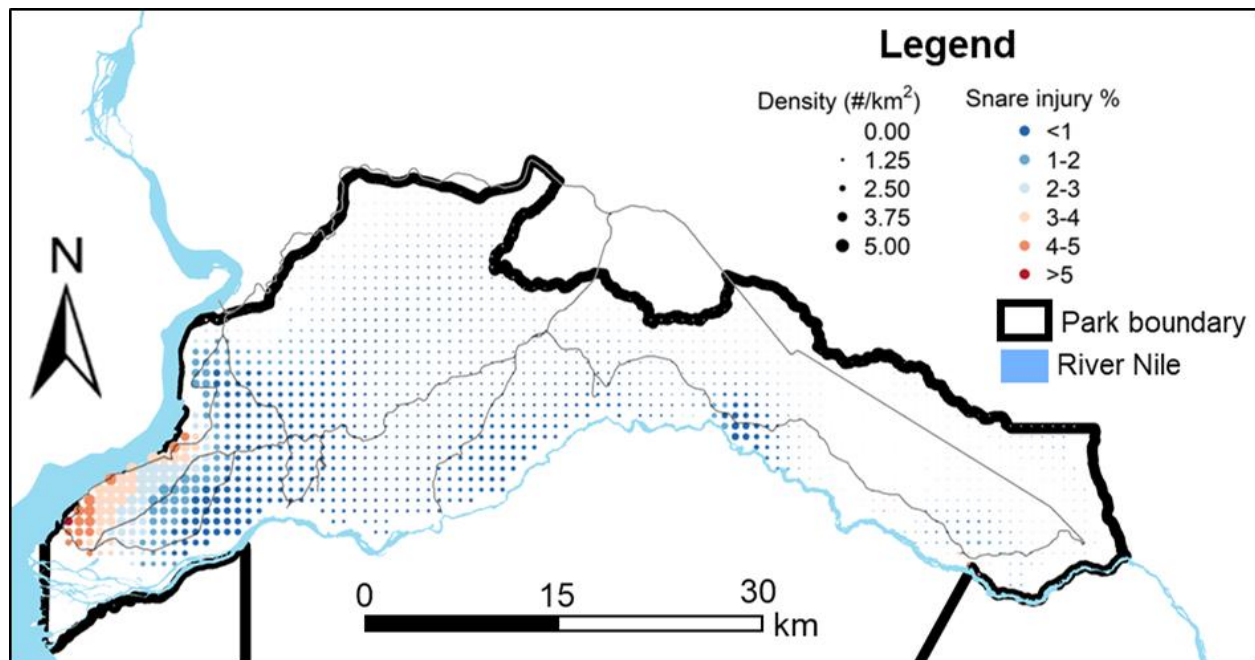


Figure 3.3. Posterior predictive map of realized density and prevalence of giraffes (*Giraffa camelopardalis rothschildi*) living with snaring injuries in Murchison Falls National Park, Uganda between June and August 2019. Grid cell resolution was 1 km $\times$ 1 km.

Discussion

Recent IUCN assessments suggest that the Rothschild's giraffes are near threatened with increasing population trends (Fennessy et al., 2018). With an estimated giraffe population of ~1,892 individuals, MFNP is a global stronghold of conservation of Rothschild's giraffes. I

observed a small proportion (~1.3%) of this giraffe population with snaring injuries, suggesting low rates of incidental poaching. All of the snaring injuries that I observed affected the legs of giraffes, with majority of individuals snared being adult and subadult males ($n = 20$ of 24). These injuries clearly altered the giraffes' mobility with reasonable expectation that there could be subsequently negative consequences for associated life history strategies such as mating and foraging. Additionally, snaring probability was positively associated with individual movement rates. The density of individuals varied spatially across the landscape, with majority of the snared individuals concentrated on the western end of the park associated with the Nile river waterways (Figure 3.3).

Within MFNP, snares are primarily set to target comparatively more abundant ungulates such as Uganda kob (~118,000 individuals), buffalo (*Syncerus caffer*; ~15,000 individuals), and hartebeest (~10,000 individuals) (Lamprey et al., 2020). Within this context, the low rates of incidental poaching of giraffes that I observed in MFNP are not necessarily surprising. Considerably low rates of giraffe poaching have been reported in other landscapes (such as Serengeti National Park, Tanzania, where 430 cases were reported between 1997 to 2010, within a population of ~3,500), despite high snare densities (Strauss et al., 2015). I emphasize however, that these relatively low rates can still have important implications for giraffe population persistence, particularly among small and fragmented populations. For instance, snaring injuries may not only affect mating ability but also cause mortality. These processes have negative consequences for recruitment and population growth given giraffes have low reproductive rates (Suraud et al., 2012; Kiffner et al., 2017).

Table 3.1. Parameter estimates (Median and 95% credible interval) from the spatial capture-recapture model fitted to giraffe (*Giraffa camelopardalis rothschildi*) photographic spatial encounter survey data between June and August 2019 in Murchison Falls National Park, Uganda. The parameters represent: probabilities for individual attributes such as population membership (ψ), sex (ψ_{male}), age class (ψ_{subadult}), presence of snaring injury (ψ_{snare}); loglinear regression coefficients for the encounter rate (α) and the scale parameter of the half-normal detection function (δ) and derived parameters of population size (N) and density (D).

Parameter	Effect	Median	95% CI
ψ		0.94	(0.90, 0.98)
ψ_{male}		0.45	(0.42, 0.48)
ψ_{subadult}		0.35	(0.32, 0.38)
ψ_{snare}		0.01	(0.01, 0.02)
α_0		-2.77	(-2.88, -2.67)
α_1	Male	0.05	(-0.09, 0.19)
α_2	Subadult	-0.05	(-0.26, 0.15)
α_3	Male x subadult	-0.22	(-0.50, 0.08)
α_4	Snare injury	0.44	(0.11, 0.77)
δ_0		1.51	(1.47, 1.57)
δ_1	Male	0.09	(0.01, 0.16)
δ_2	Subadult	-0.14	(-0.24, -0.04)
δ_3	Male x subadult	0.13	(-0.02, 0.27)
δ_4	Snare injury	0.19	(0.02, 0.39)
N		1892	(1812, 1966)
D		1.12	(1.08, 1.17)

All snaring injuries that I detected were positioned on the legs of affected giraffes (Figure 3.2). This was expected because snares are anchored to trees at the heights of target animals (Mudumba et al., 2020), species that are considerably smaller than giraffes. The natural reaction of any ensnared animal is to fight the restraint. As they fight, the snare wire bites into the skin, flesh, and eventually bone, causing fractures in extreme cases (Figure 3.2). Tightening wires against tissue during fighting can lead to restricted blood supply to legs (i.e., ischaemia), with eventual death of affected tissues (i.e., necrosis; Kalogeris et al., 2012). Acute limb ischaemia and extensive tissue necrosis cause severe pain (Simon et al., 2018) and expose the tissue to secondary bacteria or parasitic infections by dipterous fly larvae/maggots (i.e., myiasis; Francesconi & Lupi, 2012). Exertional myopathy is also possible when animals experience degenerative or necrotizing muscle damage as they struggle vigorously to escape the snare entrapment (Williams & Thorne, 1996; Cattet et al., 2008). I also observed oxpeckers (Red-billed; *Buphagus erythrorhynchus* and Yellow-billed; *Buphagus africanus*) poking into giraffe wounds to feed on maggots, flies, dead skin, and dried blood (Diplock et al., 2018). This has been suggested to prolong wound healing in large terrestrial herbivorous mammals (Weeks, 2000). Given that giraffes are tolerant of the typically symbiotic oxpeckers, which constantly feed on their open wounds (Diplock et al., 2018), the likelihood of wound healing is minimal even with medical intervention (Weeks, 2000). Thus, the giraffes eventually die prematurely as a result of their snaring injury and associated secondary infections. Before death however, these snaring injuries have important implications for giraffe ecology.

Snaring injuries and associated secondary infections on giraffe legs impose movement difficulties among affected individuals. During locomotion, the injured leg or foot is unable to support the proportional body weight of the individual over the course of a stride (Basu et al.,

2019). Thus, snaring injuries negatively affect locomotor dynamics among giraffes, via distortion of the distribution of the vertical impulse (the integral of the vertical force throughout the stride duration; Griffin et al., 2004; Basu et al., 2019). The degree of movement difficulty among injured giraffes, and subsequent impacts on energy expenditure, certainly depends on level of severity of the snaring injury. For example, movement among giraffes is almost completely impaired when they lose or fracture their lower limbs as they fight snare entrapment (Figure 3.2a). Reduced giraffe movement impairs their ability to locate mates, forage, and access water sources (Innis, 1958; Dagg, 2014).

Giraffes routinely move about their landscape in pursuit of their life history requirements (Berry, 1973; 1978). I found that males had higher movement rates than females (Table 1), which may suggest that males are more likely to be injured by the indiscriminate wire snares. This result supports the observation that adult males ($n = 12$) and subadult males ($n = 8$) were caught more often by wire snares. This observation is consistent with existing studies demonstrating that male giraffes had comparatively higher movement rates than females in other landscapes (Fennessy, 2009; Bercovitch & Berry, 2013; Strauss, 2014; Muneza et al., 2017). The fact that males move more than females likely relates to establishing dominance and seeking mates among several groups within the landscape (Berry, 1973; 1978; Dagg, 2014). Female giraffes adopt more philopatric lifestyles to protect juveniles within matrilineal-based groups (VanderWaal et al., 2013). I therefore infer that lower movement rates might reduce the risk of encountering wire snares. There is a possibility that the observation of fewer females ($n = 3$) with snaring injuries could relate to sex differences in movement rates, but additional studies would be needed to investigate this point. Such patterns where males are at higher risk of being caught by snares are common among sexually-dimorphic mammal species (Holmern et al., 2006;

Strauss et al., 2015). Male-biased impacts of human disturbances (including poaching) can lead to female-biased sex ratios and selective loss of secondary sex characteristics of affected individuals within several large mammal populations (Setsaas et al., 2007; Ndibalema, 2009; Marealle et al., 2010).

I also detected a clear spatial pattern in the configuration of giraffes with snaring injuries at the population-level. The highest prevalence of giraffes with snaring injuries was in the western end of MFNP, particularly in the delta associated with the confluence of the Albert and Victoria Nile rivers (Figure 3.3). Correspondingly, this area had the highest overall realized giraffe density (Figure 3.3). Recent evidence demonstrates that this area of MFNP is a snaring hotspot, with a density of ~ 5 snares/km² (Mudumba et al., 2020). Given that this area provides the main water source within the landscape, it attracts a host of animals including antelopes, the primary targets of subsistence poachers. Therefore, it is likely that poachers set more snares in this section of the park to maximize their yield (Mudumba et al., 2020). The waterways are also a primary pathway of poachers into MFNP (Figure 3.1). Given the high giraffe density adjacent to the river, a higher proportion of the population is exposed to the risk of incidental poaching. I conducted the photographic spatial encounter surveys during the dry season, therefore did not include the effect of season in my analyses. Recent investigations suggested a male-biased seasonal partial migration of giraffes within MFNP (Brown & Bolger, 2020). The predictions of spatial variation of incidental poaching among giraffes might therefore reflect dry season dynamics (*sensu* Muneza et al., 2017). Additional research examining seasonal dynamics of incidental poaching of giraffes and other large mammals could detect variable spatial patterns.

This study represents the first application of SCR modelling to quantifying the prevalence of snaring injuries in a giraffe population. These techniques could be similarly used across other

individually recognizable species for which poaching pressure is a threat. Although a low proportion of the giraffe population was observed with a snaring injury, impacts of living with a snaring injury are broad and may have direct implications for individual functional ecological processes such as foraging and mating (Gray et al., 2017). The individual-level consequences of snaring injuries among MFNP giraffes could potentially scale to the population level when a large proportion of individuals is affected. This is likely given the very high rates of snaring in MFNP (Mudumba et al., 2020). Quantifying the consequences of snaring injuries among affected giraffes was beyond the scope of this study but would provide useful information related to ecological and behavioral modifications resulting from living with snaring injuries. Thus, an important area of future inquiry is the examination of both the short- and long-term physiological, morphological, and ecological effects of snaring injuries among giraffes and other large mammals that suffer similar fates from incidental poaching.

CHAPTER 4: EXAMINING THE PHYLOGENETIC AND ALLOMETRIC STRUCTURING OF MAMMAL ACTIVITY

Abstract

In promoting coexistence, sympatric species often partition shared resources along spatiotemporal domains. Similarly sized and phylogenetically-close species, for instance, partition times of day in which they are active to limit interference competition. In these ways, daily activity schedules of sympatric species are often characterized by patterns of high and low activity, associated with their active and passive behavioral states. Within this context, the proportion of time a species spends active in a day is defined as its daily activity level.

Foundational research identified body mass as a primary determinant of species activity levels. Given that variation in species body mass has evolutionary underpinnings, species activity levels within animal communities might be structured by phylogeny. However, few studies have tested this hypothesis across animal communities, and none among medium to large mammals. I used multiple linear regression and Phylogenetic Eigenvector Mapping (PEM) to quantify relative contributions of phylogeny and body mass in predicting activity levels in a community of 22 sympatric mammal species in Murchison Falls National Park, Uganda. The species in this community spanned three orders of magnitude in body mass and belonged to 15 taxonomic families within eight orders. My models showed that phylogeny was a strong predictor ($R^2 = 79.6\%$) of variation in species activity levels whereas body mass had comparatively weak predictive power ($R^2 = 3.5\%$). Furthermore, including variation in body mass unexplained by phylogeny as a predictor in the phylogenetic model of species activity levels improved its predictive power ($R^2 = 83.6\%$). My analysis highlights the importance of phylogeny in predicting species traits such as activity levels in diverse mammal communities. Within this

context, I showed that phylogeny is a stronger predictor of mammal activity levels than species body mass. I explored the implications of these results for temporal niche partitioning, species coexistence, and community assembly.

Introduction

Species coexistence in animal communities is often facilitated by niche partitioning across spatio-temporal domains (Schoener, 1974; Amarasekare, 2003; Laporta & Sallum, 2014). Spatially, animals often partition niches via movements including dispersal and migration (Jeltsch et al., 2013). When spatial partitioning is not possible, animals may partition time by altering their activity schedules (Schoener, 1974; Walter, 1991; Richards, 2002; Bennie et al., 2014). Such temporal niche partitioning can minimize overlap in activity and thereby reduce interference competition among similarly sized and phylogenetically-close species (Kronfeld-Schor et al., 2001; Kronfeld-Schor & Dayan, 2003). Similarly, many prey species evolved to be active when their predators are not, to minimize predation risk (Schoener, 1974; Kronfeld-Schor & Dayan, 2003). Further, increased nocturnality has been detected among a number of animal species and interpreted as a strategy to avoid anthropogenic disturbance (Carter et al., 2012; Gaynor et al., 2018; Patten et al., 2019). Thus, competition, predation, and anthropogenic disturbance are forces that drive temporal variation in species activity (Schoener, 1974; Kronfeld-Schor & Dayan, 2003).

Through their life history, animals structure their activity schedules with both active and passive behaviors (Halle & Stenseth, 2000). Active behavioral states include foraging, reproduction, care for young, or predator avoidance, whereas passive states include resting and sleeping (Halle & Stenseth, 2000). In deciding when to be active, animals navigate potentially fitness-compromising trade-offs that partly reflect adaptability to environmental variability over

time (Enright, 1970; Halle, 2000; Vazquez et al., 2020). For example, foraging activity is required for animal sustenance and survival (Moermond, 1990) but also carries potential costs incurred from risks of inter- and intra-species interactions such as competition and predation (Halle & Stenseth, 2000; Downes, 2001). Animals routinely make such trade-offs within ecological communities that are allometrically and phylogenetically diverse. The proportion of time an animal spends active in a day (cf. activity level; Rowcliffe et al., 2014) has been adopted as a critical metric for examining tradeoffs within species activity schedules (Rowcliffe et al., 2014).

Body mass has been identified as a predominant factor determining species activity levels (Peters, 1983; West et al., 1997; Brown et al., 2004). The active behavioral states that constitute an animal's activity level and underlying schedule are constrained by body mass, which partly determines the rate at which animals acquire, process, and transform energy (Smith & Lyons, 2011). Additionally, species differences in body mass are related to their evolutionary relationships as revealed by phylogeny (Smith & Lyons, 2011). Thus, the fact that variation in species body mass has evolutionary underpinnings suggests that temporal partitioning of activity within communities might in turn be structured by species phylogenies. However, few studies have formally evaluated the hypothesis that phylogeny predicts species activity (Webb et al., 2002). Communities of medium to large mammals present an opportunity to pursue this line of inquiry. Phylogeny reflects evolutionary differences among species, which may be related to ecological processes and dynamics (Felsenstein, 1985; Harvey & Pagel, 1991; Faith, 1992). Therefore, an understanding of mechanisms generating species differences in timing of their activity must be inclusive of the evolutionary components of species divergence (Webb et al., 2002; Narwani et al., 2015). Thus, an investigation of the relative contributions of body mass and

phylogeny to predicting patterns of variation among species activity levels may reveal the ecological and evolutionary processes underlying animal coexistence and community assembly.

Over 200 million years ago in the late carboniferous period, mammals evolutionarily radiated into approximately 6,399 extant species (Burgin et al., 2018). Species in the Class Mammalia span eight orders of magnitude in body mass (Baker et al., 2015) and exhibit a variety of activity levels and schedules (Halle & Stenseth, 2000). Using sympatric mammals as research subjects, I explored; *i*) the relative contributions of phylogeny and body mass in predicting variation in mammal activity levels and *ii*) whether evident differences in mammal activity levels are phylogenetically structured. I examined these questions in a diverse mammal community in Murchison Falls National Park, Uganda. The species included in this analysis varied broadly in taxonomy, body mass, and activity. I investigated pairwise overlap among activity schedules of species within the same taxonomic orders to assess temporal niche partitioning. My results provide insights into the role of phylogeny and body mass in structuring mammal activity within communities, with implications for temporal niche partitioning and species coexistence.

Methods

Study area

I conducted this study in Murchison Falls National Park (MFNP), located in northwestern Uganda (Figure 4.1). Covering an estimated land area of approximately 3,898 km², MFNP is the largest national park in Uganda. A section of the River Nile (i.e. Victoria Nile) flowing from the east to west bisects MFNP into northern and southern sections. The vegetation of the southern section comprises dense woodlands, wooded grassland savannahs, riverine forest, and tropical high forest. The northern section comprises open grasslands, acacia (*Acacia spp.*) woodland, and

borassus (*Borassus aethiopum*) woodland as the dominant vegetation types (Figure 4.1).

Murchison Falls National Park has a hot and dry tropical climate characterized by wet (April to May, and September to November) and dry seasons (December to February, and June to August). It also supports a diversity of mammals consisting of approximately 76 mammal species (Mudumba et al., 2020).

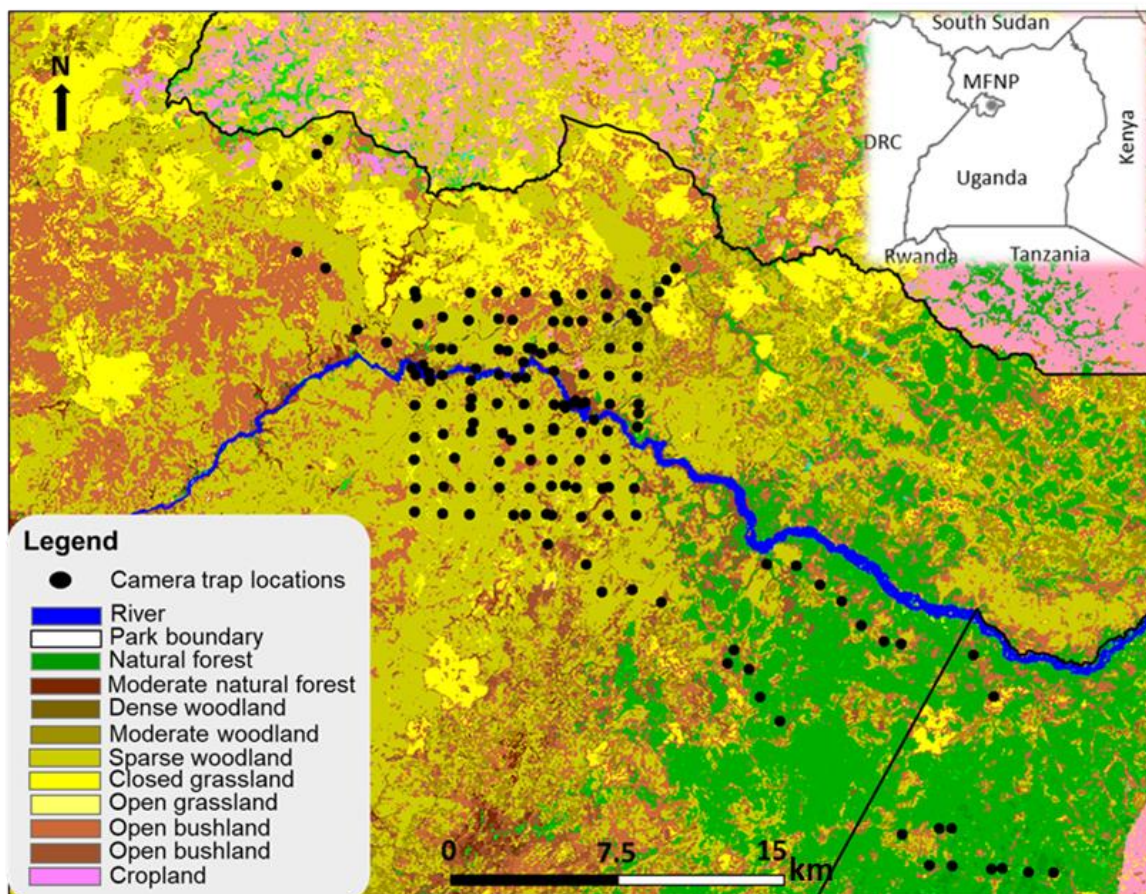


Figure 4.1. Layout of camera traps used to study mammal activity in Murchison Falls National Park (MFNP), Uganda between May 2012 and August 2013. Inset, location of MFNP in Uganda, the grey dot signifies the extent of the study area covered by the survey.

Mammal surveys

I deployed camera traps (Ltl-5210A Acorn) at 144 sites between May 2012 and August 2013 to obtain records of medium to large mammal species activity (Figure 4.1). I placed cameras systematically on a grid of 1.5 km x 1.5 km resolution (Figure 4.1). I also placed cameras at some opportunistic locations considered important landscape features for mammals (such as water pools, river, trails, salt licks). Via this strategy, I ensured broad coverage of all habitat types in the study area (Figure 4.1). I mounted camera traps on tree trunks, at most one meter off the ground to capture species of varied sizes, and to avoid destruction of the cameras, particularly by spotted hyenas (*Crocuta crocuta*). Given this height, I slightly tilted the traps downwards to enable detection of a range of mammal species (Majelantle et al., 2020). Additionally, I avoided facing cameras directly at vegetation to minimize false triggers from vegetation movement in windy conditions. I programmed the cameras to take three photos per trigger with a one-minute lapse between triggers (Lepard et al., 2018). I conducted this survey in a backcountry area of MFNP where recreational human activity and park staff residences were absent. I set the traps unbaited and deployed for the entire 16-month survey period.

I assumed independence in species detections by enforcing a 30-minute temporal window between intraspecific detection events at each camera location, unless individuals of the same species were distinguishable (Kelly & Holub, 2008; Davis et al., 2011; Monterroso et al., 2013). I then modelled activity levels for species with ≥ 30 detections across the camera trapping period as described below (cf. Cid et al., 2020). I obtained body mass data for all species from Faurby et al. (2019) and adapted the phylogenetic tree from the super tree of Fritz et al. (2009).

Estimating mammal activity levels

I fit circular von Mises kernels to the time of day associated with each independent animal detection event and generated activity levels (A) for the 22 species. I defined activity levels as the portion of the 24-hour daily cycle the mammals spent active (cf. Rowcliffe et al., 2014). Activity levels corresponded to area under the kernel density curve for each species, estimated with 95% confidence limits generated with 1000 bootstraps (Rowcliffe et al., 2014).

Modelling

I investigated the effect of body mass and phylogeny on species activity levels using Phylogenetic Eigenvector Maps (PEM; Guenard et al., 2013) and linear regression. I omitted the effect of weather and season because I observed no differences in species activity schedules across the dry and rainy seasons (Figure S1). The PEM decomposes the phylogenetic structure of the mammal community into an influence matrix used to calculate eigenvectors, ultimately used as predictors in multiple linear regression (see Griffith & Peres-Neto, 2006). For a set of n species, PEM returns a matrix encompassing $n - 1$ eigenvectors that can be used as predictors in multiple linear regression to represent phylogenetic structure in traits (Guenard et al., 2013). Each eigenvector describes a pattern of phylogenetic variation stemming from the structure of the phylogenetic tree, and that is orthogonal (linearly independent) with respect to the other eigenvectors in the set (Figure 4.2; detailed in Guenard et al., 2013). Additionally, patterns represented by PEM are based on information from the typology and the branch length of the phylogenetic tree.

I modeled the influence of body mass on species activity levels as;

$$\log(A_i) \sim \varphi_0 + \varphi * \log(M_i) + \tau_i \quad (\text{eqn 1});$$

where A_i is the activity level for species i , φ_0 is the intercept, φ is the regression parameter associated with the species body mass M_i and τ_i is the residual term.

To compare the body mass model above to a phylogenetic model, I fit a separate model of species activity levels as;

$$\log(A_i) \sim \psi_0 + \boldsymbol{\psi} * V_i + \eta_i \quad (\text{eqn 2});$$

where A_i is the activity level for species i , ψ_0 is the intercept, $\boldsymbol{\psi}$ is the vector of regression parameters associated with the phylogenetic eigenvectors V_i and η_i is the residual term. I then compared the variation in species activity levels explained by body mass and phylogeny using R^2 values from eqn 1 and eqn 2 respectively.

Given that body mass is structured with respect to phylogeny, I investigated the effect of phylogeny on species body mass in the study system as;

$$\log(M_i) \sim \beta_0 + \boldsymbol{\beta} * V_i + \varepsilon_i \quad (\text{eqn 3});$$

where M_i is the mass for species i , β_0 is the intercept, $\boldsymbol{\beta}$ is the vector of regression parameters associated with the phylogenetic eigenvectors V_i and ε_i is the residual term, which represents variation in body mass not controlled by phylogeny.

Finally, I sought to understand whether residual variation in body mass from eqn 3 (i.e., variation in body mass unrelated to phylogeny) had an additive effect in the phylogenetic activity model in eqn 2. Thus, I fit this model as;

$$\log(A_i) \sim \alpha_0 + \boldsymbol{\alpha} * V_i + \varepsilon_i + \zeta_i \quad (\text{eqn 4});$$

where A_i is the activity level for species i , α_0 is the intercept, $\boldsymbol{\alpha}$ is the vector of regression parameters associated with the phylogenetic eigenvectors V_i , ε_i are the residuals from the model in eqn 3, and ζ_i is the residual term. I conducted this analysis on the logarithm of body mass and

activity levels to reduce skew in the data and to linearize the relationship between them (Moll et al., 2019). For all phylogenetic models (equations 2 - 4), I conducted model selection using step-wise variable addition based on corrected Akaike Information Criterion (AICc) to choose the best set of eigenvectors (i.e., those that minimized AIC; Hurvich & Tsai, 1993; Yamashita et al., 2007). The selected eigenvectors highlight the phylogenetic patterns significant to predict the variability in body mass and activity levels across species respectively (Figure 4.2).

Estimating activity overlap

I grouped species according to their taxonomic orders and estimated within-order pairwise activity overlap. I tested for activity overlap among the species using the coefficient of overlap (Δ ; Ridout & Linkie, 2009). The Δ value ranges from 0 (for completely dissimilar curves) to 1 (for identical curves). I generated 95% confidence limits for each overlap estimate using 10,000 smoothed bootstraps. I performed a Watson's two-sample test of homogeneity using the $\alpha \leq 0.05$ level to test for statistical significance in differences between species activity schedules.

I conducted all analyses using the R language and environment v. 4.0. (R Core Team, 2020) and R packages activity (v.1.3.; Rowcliffe, 2019), ape (v.5.0.; Paradis & Schliep, 2018), CircStats (v.0.2-6.; Lund & Agostinelli, 2018), MPSEM (v.0.3-6.; Guenard & Legendre, 2019), and overlap (Ridout & Linkie, 2009).

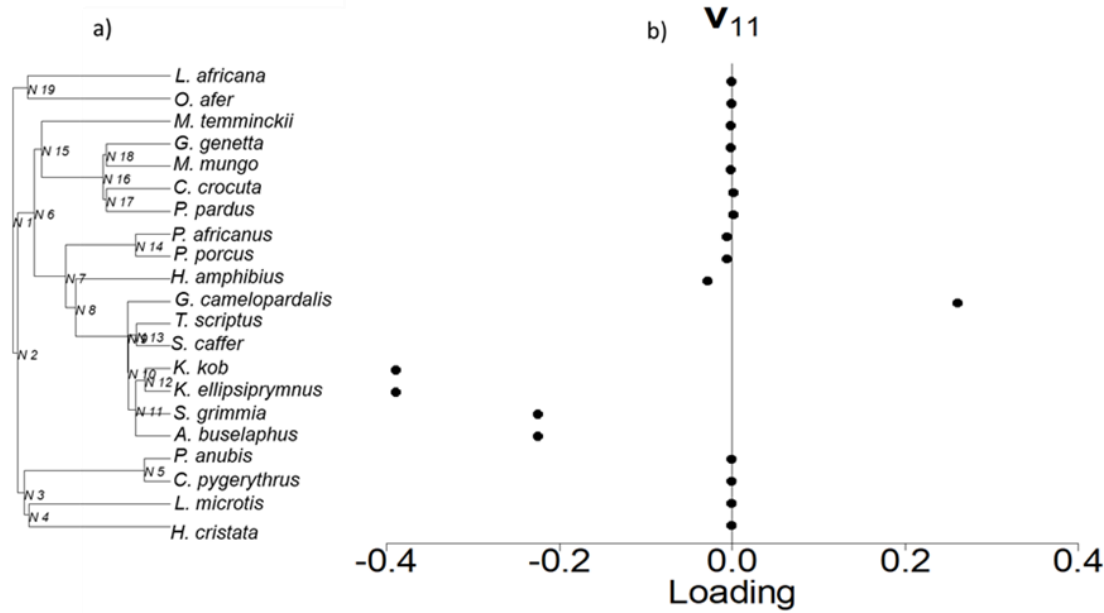


Figure 4.2. The phylogenetic approach used in modelling mammal activity levels in Murchison Falls National Park, Uganda. A phylogenetic tree (a) is used to calculate a phylogenetic eigenvector map (b) whose eigenvectors are used together with species traits as descriptors of activity level in a linear regression (see Guenard et al., 2013 for a complete description). In the phylogenetic tree, the N_i are tree nodes. In the phylogenetic eigenvector map, the round dots represent species loadings on an eigenvector (e.g. V_{11} chosen as an example).

Results

I analyzed the relationship between body mass, phylogeny, and activity levels of 22 sympatric mammal species from eight taxonomic orders and 15 families (Figure 4.3) using 23,758 independent observations from the camera traps. The most commonly detected species were Uganda kob (*Kobus kob*, $n = 4,833$ detections) followed by hippopotamus (*Hippopotamus amphibious*, $n = 4,166$ detections, Table S1). The least detected species included ground

pangolin (*Manis temminckii*, $n = 31$ detections) and banded mongoose (*Mungos mungo*, $n = 38$ detections).

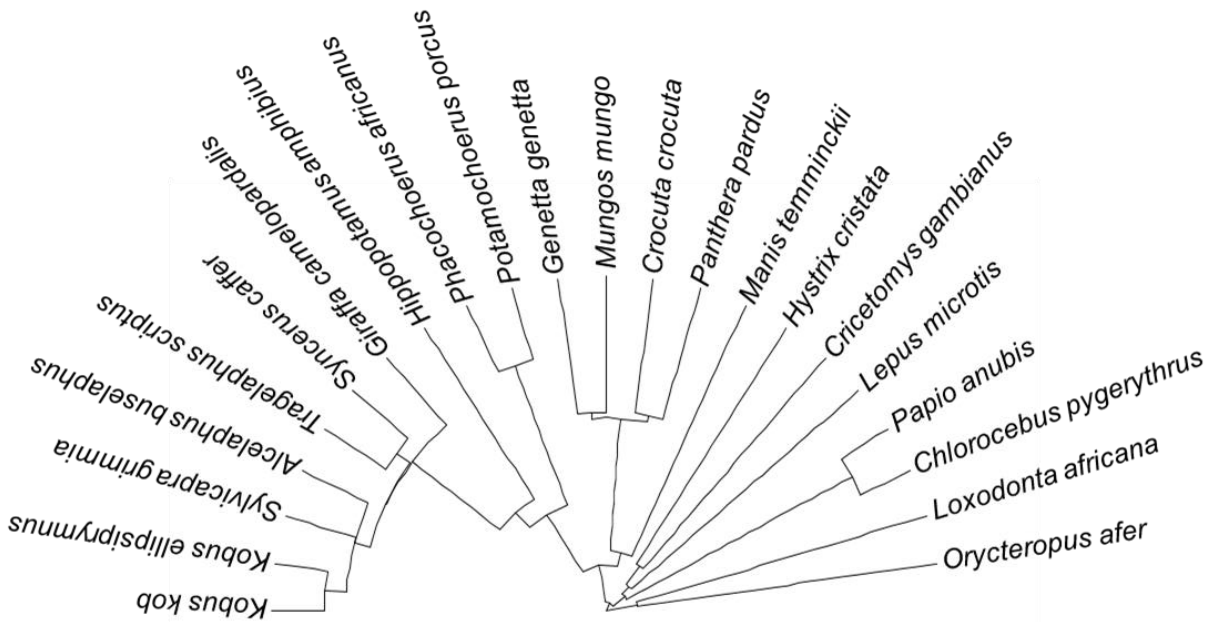


Figure 4.3. Phylogeny of the 22 mammal species observed in Murchison Falls National Park, Uganda from a camera trapping survey conducted between May 2012 and August 2013. The tree is adapted from Fritz et al. (2009) after removing species that were not observed in the current surveys.

Activity level estimates varied across species, both within and across taxonomic orders (Figure 4.4). Among carnivores, banded mongoose (*Mungos mungo*) were most active, with approximately 17 hours of activity in a day ($A = 0.71$, 95% CI 0.42–0.81; Figure 4.4). The remaining carnivores spent approximately 11 hours active per day (Figure 4.4, Table S1, Figure S2). Among the Cetartiodactyls, hartebeest (*Alcelaphus buselaphus*) was the most active species, spending approximately 18 hours active per day ($A = 0.76$, 95% CI 0.65–0.85; Figure 4.5). The least active species within the order Cetartiodactyla was the bush duiker (*Sylvicapra grimmia*)

spending approximately 9 hours active ($A = 0.38$, 95% CI 0.28–0.57). Elephants (*Loxodonta africana*) were equally active as hartebeest, whereas armadillos (*Orycteropus afer*) were the least active among all species ($A = 0.35$, 95% CI 0.31–0.44, approximately 8 hours active; Table S1, Figure 4.5).

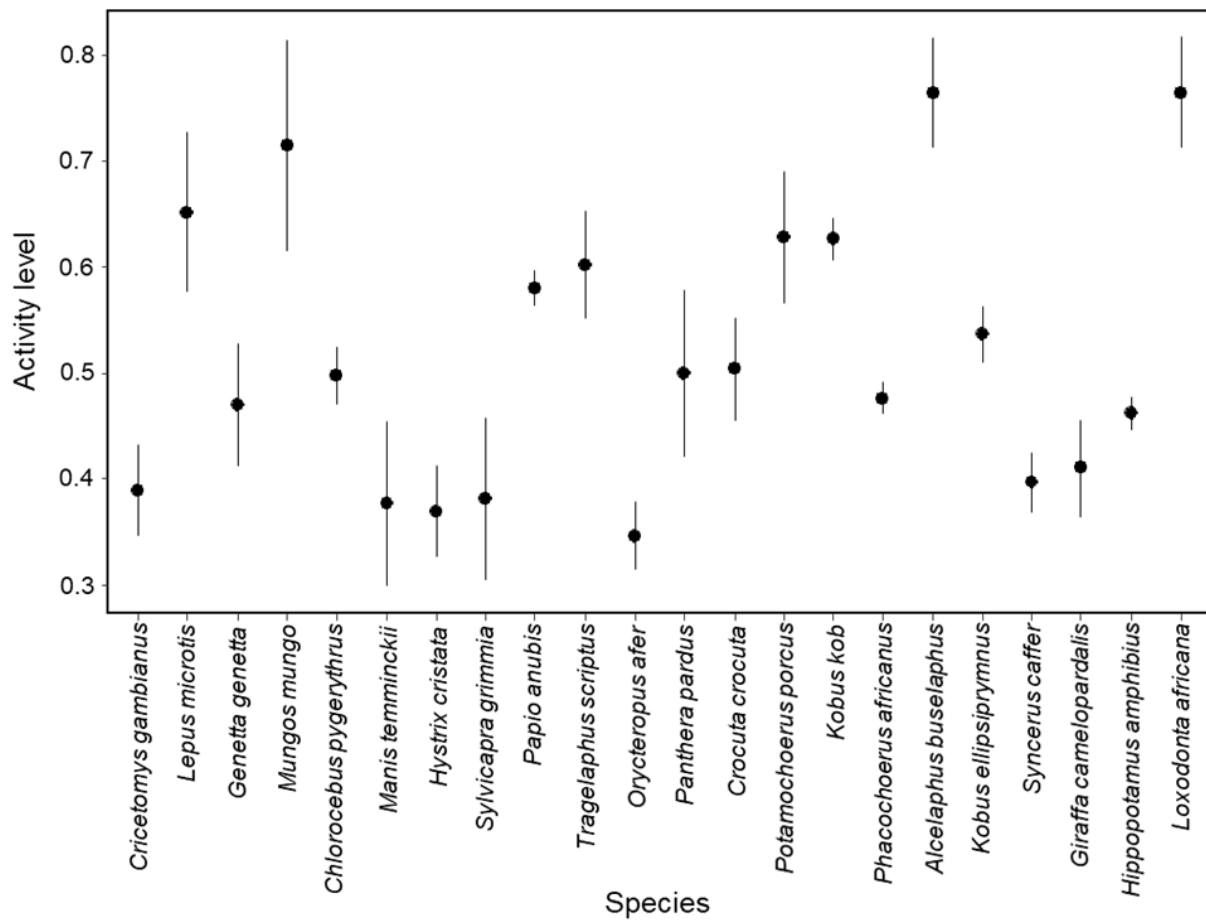


Figure 4.4. Activity level estimates of 22 mammal species estimated using camera trap temporal records from Murchison Falls National Park, Uganda obtained between May 2012 and August 2013. Species are arranged according to their increasing body mass.

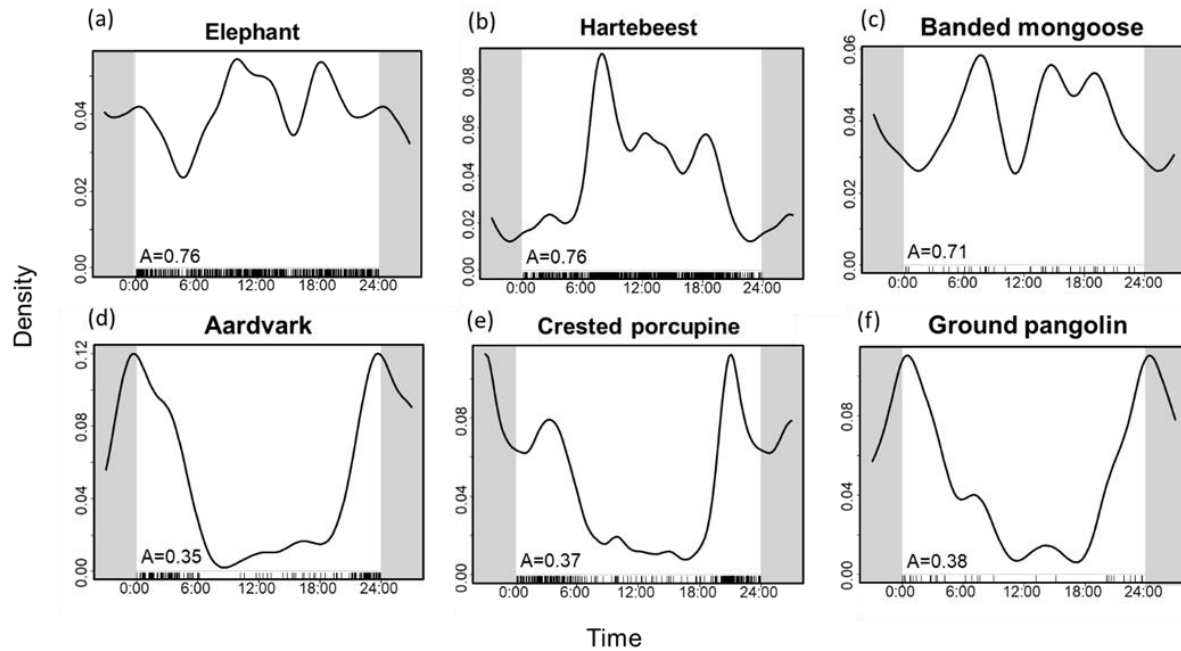


Figure 4.5. Activity schedules of mammal species with the highest (a, b, c) and lowest (d, e, f) activity levels (A) in Murchison Falls National Park, Uganda, estimated using camera trap temporal records. The activity curves are fitted circular von Mises kernel density curves showing patterns of species activity across a 24-hour daily cycle.

I obtained 21 phylogenetic eigenvectors ($V_1 - V_{21}$) from the subtree of 22 species. Seven eigenvectors in the phylogenetic model (eqn 2; Table S2) explained 79.6% of the variation in species activity levels ($P < 0.001$), whereas the body mass model (eqn 1) explained only 3.5% ($P > 0.05$), based on model R^2 values. Six eigenvectors explained 71.7% of the variation in body mass (eqn 3; $P < 0.001$; Table S3). The variation in body mass unrelated to phylogeny improved the predictive ability of the phylogenetic model (eqn 4) of species activity levels ($R^2 = 83.6\%$; $P < 0.01$; Table S4).

Across all taxonomic orders, we detected considerable pairwise overlap among species activity schedules (Figure 4.6, Table S5; Figure S3). Species pairs with highly overlapping

activity schedules included olive baboon (*Papio anubis*) and vervet monkey (*Cercopithecus pygerythrus*), Uganda kob and waterbuck (*Kobus ellipsiprymnus*), Uganda kob and hartebeest, and waterbuck and hartebeest which all had overlap coefficients of at least 0.90 (Range 0.90-0.91; Table S5; Figure 4.6). On the other hand, species pairs with the least overlapping activity schedules included hippopotamus and warthog (*Phacochoerus africanus*), giraffe (*Giraffa camelopardalis rothschildi*) and hippopotamus, bush duiker and hippopotamus, all with overlap coefficients of less than 0.4 (Range 0.33-0.35; Table S5; Figure 4.6). Despite the high overlap among activity schedules across several species, the Watson's test indicated significant differences in the majority of pairwise species activity schedule comparisons ($P < 0.05$, Table S5).

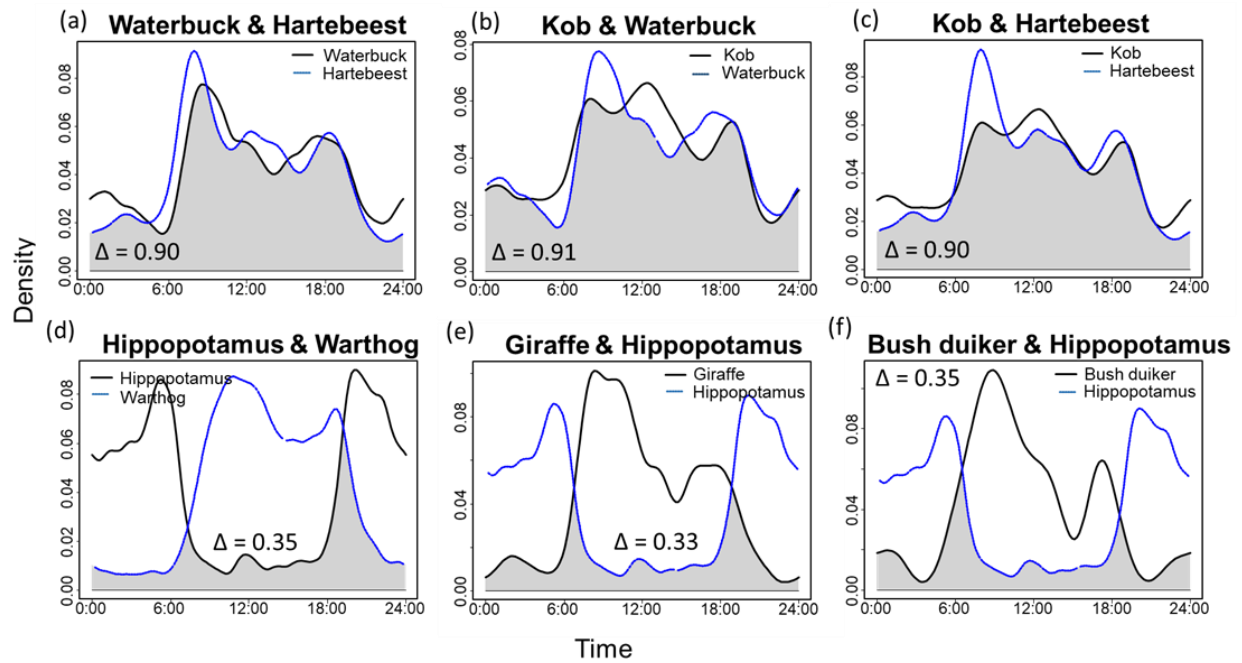


Figure 4.6. Pairwise overlap of activity schedules between selected mammal species in Murchison Falls National Park, Uganda, as estimated using camera trap temporal records. The highest activity overlap was between a) waterbuck (*Kobus ellipsiprymnus*) and hartebeest (*Alcelaphus buselaphus*), b) kob (*Kobus kob*) and hartebeest, and c) kob and water buck all with overlap coefficients of 0.9 (95% CI 0.87–0.94, Table S5). The least activity overlap was between d) hippopotamus (*Hippopotamus amphibius*) and warthog (*Phacochoerus africanus*), e) hippopotamus and giraffe (*Giraffa camelopardalis rothschildi*), and f) hippopotamus and bush duiker (*Sylvicapra grimmia*) all with overlap coefficients of 0.3 (95% CI 0.24–0.46, Table S5).

Discussion

I used phylogenetic eigenvector mapping and linear regression modelling to explore the role of body mass and phylogeny in predicting patterns of activity level variation in a diverse mammal assemblage. I highlighted a significant variation in species activity levels across the

phylogeny. However, activity levels of phylogenetically-close species tended to be more similar, especially within taxonomic orders with high numbers of species. Comparatively, there was less influence of body mass in explaining species activity levels. This was exemplified by the general lack of a trend between body mass and activity levels among species across the phylogeny (Figure 4.4). Exploring such phylogenetically-explicit relationships among species traits is important to quantify variation related to phylogenetic history (Desdevises et al., 2003), given that species radiate from a common ancestor (Burgin et al., 2018). Within this context, residual variation in species trait represents independent evolution of the trait within each species (Diniz-Filho et al., 1998; Desdevises et al., 2003). This analysis illustrates the broad applicability and relevance of multispecies phylogenetically-explicit modelling in exploring patterns of species traits. Such methods could be employed to examine multiple factors that facilitate species assembly and coexistence as they relate to phylogenetic structure within communities across other taxonomic groups.

My phylogenetically-explicit models detected a significant influence of phylogeny on both mammal body mass and activity levels, highlighted by phylogenetic eigenvectors explaining over 70% of the variation observed in both variables. I did not detect a significant influence of body mass on mammal activity levels. I interpret this result to be indicative of phylogenetically-distant species showing no clear patterns between body mass and activity levels (Figure 4.4). Body mass may nevertheless have an effect if modelled across a range of phylogenetically-close species, say within one taxonomic order in which species have widely different body masses and activity levels. This may reduce the correlation between body mass and phylogeny, and thus allow detection of an effect of body mass. In this regard, the observed statistical significance of the residual body mass (after accounting for the variation explained by

phylogeny) on activity levels is not surprising (Table S4). Additionally, recent studies detected strong relationships between body mass and mammal activity levels when phylogeny is not included among the predictors (e.g., Rowcliffe et al., 2014; Ramesh et al., 2015). This analysis thus highlights the need to control for phylogeny when exploring interspecific trait variation in diverse communities. My results build upon initial work on rodents to reveal the importance of phylogeny in structuring activity in mammal communities (Roll et al., 2006). However, additional research among a broader range of species is required to further highlight the role of species body mass and evolutionary relationships in the generation and maintenance of species differences in activity, temporal niche partitioning, and species coexistence.

I found that elephants and hartebeests had the highest activity levels of all species (Figure 4.4, 4.5a, b). Among the carnivores, my results showed that banded mongoose had higher activity levels than the larger genet (*Genetta genetta*), hyena, and leopard (*Panthera pardus*) (Table 4.1, Figure 4.5c, Figure S3). Collectively, these results highlighted no consistent patterns between species body mass and activity levels across the phylogeny (Figure 4.4). This explains my observation that body mass explained a small proportion in species activity levels across the phylogeny. A critical difference I observed among carnivore activity is that banded mongoose are cathemeral, exhibiting peak activity during day light hours. Whereas genet, hyena, and leopard are strictly nocturnal species (Figure S2). This temporal partitioning of activity among carnivores aligns with differences in foraging strategies, and has been suggested to promote coexistence (Hayward & Slotow, 2009). Mongoose are predominantly insectivorous, but could become prey for larger nocturnal carnivores, hence their need to maintain low activity during the night. The species with the lowest estimated activity levels were all obligate nocturnal species (i.e., armadillo (*Orycteropus afer*), crested porcupine (*Hystrix cristata*), and ground pangolin

(*Manis temminckii*; Figure 4.5d, e, f). These animals are shy and elusive burrowing species, which spend the majority of the day in underground tunnels (Felicioli et al., 1997; Nowak, 1999; Taylor & Skinner, 2003; Tabruce et al., 2008). Consequently, their activity estimates may therefore be interpreted as nocturnal given their biased detection above ground.

Despite the high overlaps, differences between activity schedules of a majority of phylogenetically-close species were statistically significant (e.g. Figure 4.6a, b, c). A close examination of activity curves for these species revealed considerable variations in their peak activity times (Figure 4.6, Figure S3). Such variation suggests that temporal niche partitioning among phylogenetically-close species is only possible within specific times of day, perhaps highlighted as times of peak activity. Given that phylogenetically-close sympatric species use similar resources (Daan, 1981; Roll & Dayan, 2002), it is necessary for them to maximize their resource consumption in times when their relatives' activity is low (Kronfeld-Schor & Dayan, 2003). Variation in species times of peak activity is critical in minimizing interspecific encounters and interference competition, and thus can facilitate coexistence (Schoener, 1974; Daan, 1981; Roll & Dayan, 2002). My results show that hippopotamus had the least activity overlap with several species, including warthog, giraffe, and bush duiker ($\Delta < 0.5$; Figure 4.6d, e, f; Table S5; Figure S3). I attribute this result to the fact that hippopotamus predominantly inhabit aquatic environments during the day, but forage on land at night (Eltringham, 1999). The nocturnal terrestrial activity of hippopotamus therefore minimizes potential for activity overlap with diurnal phylogenetically-close relatives.

In conclusion, I detected a statistically significant influence of phylogeny on species body mass and activity levels indicative of a phylogenetic structuring of these traits within a diverse mammal community. Given these phylogenetic links, it is critical to consider evolutionary

relatedness when exploring relationships between activity and body mass across species. This is attributed to the fact that trait values may be autocorrelated at different phylogenetic distances (Diniz-Filho & Torres, 2006). Therefore, partitioning variation in a trait related to phylogeny accounts for the common ancestry with other species (Pignata & Diniz-Filho, 1996). Taken together, the findings of this study suggest that evolutionary relatedness can be a useful pathway to reveal mechanisms underlying structuring of activity, coexistence as well as patterns of assembly in animal communities. In an applied context, insights from this research may be useful when identifying conservation and management priorities based on the phylogenetic comparison of species activity.

CONCLUSION

In this dissertation, I explored the ecological, evolutionary, and anthropogenic factors that underlie mammal communication, sociality, activity, and assembly. In chapter one, I explored modalities via which giraffes exchange vital information among themselves. Studying communication among giraffes is a challenging task, as highlighted by only 21 relatable studies published in the last six decades. Given that it is now known that giraffes exchange vital information via visual, olfactory, and auditory pathways, future studies need to design experiments to test hypotheses examining the propagation and context of communication signals within giraffe communication systems. In chapter two, I found a pervasive incoherence in the ways researchers define ungulate group sizes both within and between species across study sites. To harmonize the progress of research dependent on the evaluation of animal grouping, further research needs to design frameworks to integrate fundamental aspects of sociality across social animals. This is needed to provide coherence in the ways researchers study patterns in animal grouping. Coherence in defining animal grouping is a challenge that needs to be embraced to facilitate study replication and evaluation of theory. In chapter three, I examined the effects of incidental poaching on giraffes in Murchison Falls National Park, Uganda. Although a low proportion of the population lived with snaring injuries, there are secondary effects of living with snaring injuries. Therefore, to appreciate the extent to which incidental poaching affects large mammals, researchers and managers need to constantly monitor populations to obtain the number of individuals that die and those that live with snaring injuries. Additional research examining the individual effects of living with a snaring injury and how these scale to the population is a critical need, especially in landscapes where wire snare poaching is highly prevalent. In the fourth chapter, I investigated the role of phylogeny and body mass in predicting

mammal activity levels, and discussed implications for temporal niche partitioning. I showed that phylogeny is a stronger predictor of mammal activity levels than body mass. My results highlight the need to incorporate phylogeny when investigating relationships among traits across several species, given species share phylogenetic history. By doing so, ecologists will uncover true relationships, independent of species shared evolutionary history.

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