SPATIAL ECOLOGY METHODS AND APPLICATIONS TO LARGE CARNIVORE CONSERVATION IN KENYA

By

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ABSTRACT

In this dissertation, I develop and apply various spatially explicit methods to quantify ecological conditions and space use of large carnivores in multifunctional landscapes such as protected areas and rangelands. I investigate how the social behavior and space use of several large carnivore species vary across ecological gradients within Kenyan protected areas exposed to high levels of pastoralist activity, identify avenues for future research in spatial ecology and conservation behavior, and provide methodology by which to pursue these lines of research. In Chapter Two, I develop a novel approach to land cover classification in heterogeneous savanna landscapes and apply it to the Maasai Mara National Reserve, Kenya. This Reserve is of great value for conservation, international research collaborations, and use by local pastoralists for livestock grazing. I achieve unparalleled success in distinguishing among different grass heights as well as other diverse land cover types, thus providing a valuable tool by which to extract land cover for use as a spatially explicit predictor of wildlife behavior (e.g., space use, conflict with humans) and to monitor the effect of livestock grazing intensity on grass height and cover in future studies. In Chapter Three, I use these land cover data as well as a historical database of other environmental variables, livestock abundance, and large carnivore sightings to assess how carnivores have shifted their spatial distributions and habitat selection over the years in response to the presence and abundance of livestock and herders inside the Reserve. In Chapter Four, I provide guidelines for individual identification of hyaenids using naturally occurring markings, review the substantial utility of this method in past and ongoing basic research, and identify important avenues by which to apply this method to the monitoring and conservation of wild hyaenids and the mitigation of human-hyaenid conflict in shared landscapes. In Chapter Five, I investigate the social behavior of a poorly understood and globally declining large carnivore, the striped hyena. Specifically, I conducted the first empirical study of pasting in striped hyenas and described social behavior at den sites, including the first reported case of allonursing, to show that this population is highly social and even exhibits cooperative care of offspring. The diversity of social systems observed across striped hyena populations in recent studies suggests that this species is much more behaviorally plastic than previously recognized. Overall, this dissertation contributes to our understanding of the complex relationships between carnivores' behavior and the environments in which they live, as well as how human activity mediates these interactions. Overlooking the behavioral adaptations that humans induce in large carnivores could prevent us from predicting trophic cascades that result in the loss of biodiversity and ecosystem function. Alternatively, seeking to understand these behavioral responses could facilitate the innovation of novel techniques by which to promote the coexistence of humans and carnivores in multifunctional landscapes.

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CHAPTER 1:

GENERAL INTRODUCTION

Human activity has played a tremendous role in reshaping ecosystems and accelerating the loss of biodiversity (Ceballos et al. 2015, Ellis 2015), but few taxa have been more devastatingly affected than large mammalian carnivores (Gittleman et al. 2001, Estes et al. 2011, Ripple et al. 2014, Ripple et al. 2016, Fernández-Sepúlveda & Martín 2022). Carnivores have enormous home range requirements, making them sensitive to habitat loss and fragmentation. Their wide-ranging movements and high metabolic requirements bring them into frequent conflict with humans and livestock, and they can pose threats to the safety of humans and domestic pets. Furthermore, their low densities and slow life histories render many carnivore species ill-equipped to adapt to rapid anthropogenic change. As a result, large carnivores have undergone severe geographic range contractions and global population declines, and many are now at risk of extinction (Ripple et al. 2014, Fernández-Sepúlveda & Martín 2022).

The loss of apex predators carries disproportionate consequences for biodiversity. Apex predators indirectly mediate interactions among lower trophic levels, and their removal often has substantial cascading effects on populations of sympatric wildlife and their foraging behavior (Estes et al. 2011, Ripple et al. 2014, Suraci et al. 2016, Atkin et al. 2019). These trophic cascades can even alter processes underlying disease outbreaks, invasion by nonnative species, wildfires, and carbon sequestration, as well as the composition of soil, water, and the atmosphere (Estes et al. 2011, Ripple et al. 2014). Lower trophic interactions are mediated not only by the presence and abundance of carnivores, by also by their behavior. Therefore, human activity can set off trophic cascades not only through suppressing carnivore populations or curtailing their ranges, but even through inducing behavioral changes (Suraci et al. 2019, Wilson et al. 2020), such as altered diel activity patterns, space use, or foraging (Berger 2007, Oriol-Cotterill et al. 2015a, Smith et al. 2015, Gaynor et al. 2018). However, behavioral adaptations have also proven key for the survival of carnivore populations in human-disturbed landscapes (Oriol-Cotterill et al. 2015b, Miller & Schmitz 2019, Kautz et al. 2021).

In the first two chapters of this dissertation, I examined spatial distributions of vegetation and wildlife in the Maasai Mara National Reserve, southern Kenya. The Reserve lies on land historically controlled by the Maasai tribe, in which livestock are pivotal to economics, food security, and culture (Goldman 2011, Butt 2014). Livestock grazing by local communities is legally prohibited in the Reserve and this is strictly enforced in the western part of the Reserve, whereas enforcement on the eastern side has fluctuated drastically with shifts in Reserve management, with livestock grazing intensity peaking in the dry season. In Chapter Two, I developed an innovative new methodological approach for land cover classification and apply it to generate a highly detailed land cover map of the entire Reserve. Previous mapping techniques have proven ineffective at accurately predicting grass height outside of homogenous grasslands such as pastures. In a mixed savanna landscape such as this, where grassland represents the most common cover but occurs near other diverse land cover types, this severely limits the level of detail that can be generated by land cover estimation. In this chapter, I used an iterative machine learning process to analyze multi-date remotely sensed optical and radar imagery and field data (ground-truthing) to produce a high-resolution (10 x 10 m) land cover map distinguishing twelve land cover class with an overall accuracy of 86%. We succeeded in distinguishing short, medium, and tall grass at user's accuracies of 83%, 82%, and 85%, respectively.

In Chapter Three, I examined how livestock abundance inside the eastern Reserve has differentially affected diurnal space use by lions (*Panthera leo*), cheetahs (*Acinonyx jubatus*), and black-backed jackals (*Lupulella mesomelas*). Specifically, I investigated how livestock abundance modulated carnivores' proximity to livestock grazing areas and their use of vegetative cover (derived from the map produced in Chapter Two). Livestock grazing had the strongest effect on space use by lions, who significantly increased their distance from the Reserve boundary in response to elevated livestock abundance inside the Reserve. Lions were the only species observed to show strong selection of closed habitat, as well. Lions are the dominant species in this carnivore guild but are persecuted by humans more than cheetahs or jackals are (Kissui 2008, Koziarski et al. 2016). I found no effect of livestock abundance on use of vegetative cover in any of these three carnivore species, but our inability to account for detection probability may have masked effects of habitat type. My findings show how rates of conflict with humans and intensity of persecution can modulate the effects of human activity on carnivores in shared landscapes and highlight that different carnivore species respond differently to human presence.

Anthropogenic effects on population size and behavior have been well-documented in lions (Oriol-Cotterill et al. 2015a, Riggio et al. 2018) but remain poorly understood in some carnivore species, presumably hindering their effective management and conservation. For example, striped hyenas (*Hyaena hyaena*) are difficult to observe in the wild and, as a result, population estimates are unavailable throughout much of their range and little is known about their basic behavior and ecology (Hofer & Mills 1998, AbiSaid & Dloniak 2015). Such a paucity of information can prevent us from accurately estimating their population sizes (Akçakaya et al. 2006), identifying threats to their persistence, developing and refining strategies for conflict mitigation, understanding the ecosystem service they provide, and predicting cascading effects of human-induced changes in their populations or behavior.

In the final two chapters of my dissertation, I explored how studies of individually recognizable carnivores can fill in knowledge gaps regarding their demography, dispersal, social behavior, and conflict with humans. In Chapter Four, I provided guidelines for individual recognition in aardwolves (*Proteles cristata*), spotted hyenas (*Crocuta crocuta*), brown hyenas (*Parahyaena brunnea*), and striped hyenas, and reviewed established and potential applications to basic science and conservation. Our existing knowledge of these species' ecology has been largely acquired from studies taking advantage of naturally occurring markings, such as unique coat patterns and scars. Such studies have been invaluable to conservation and management by facilitating population estimates and analysis of population connectivity, and should be applied to the identification of ecological traps (Balme et al. 2010) and investigation of intrapopulation variability in livestock depredation ("problem animals").

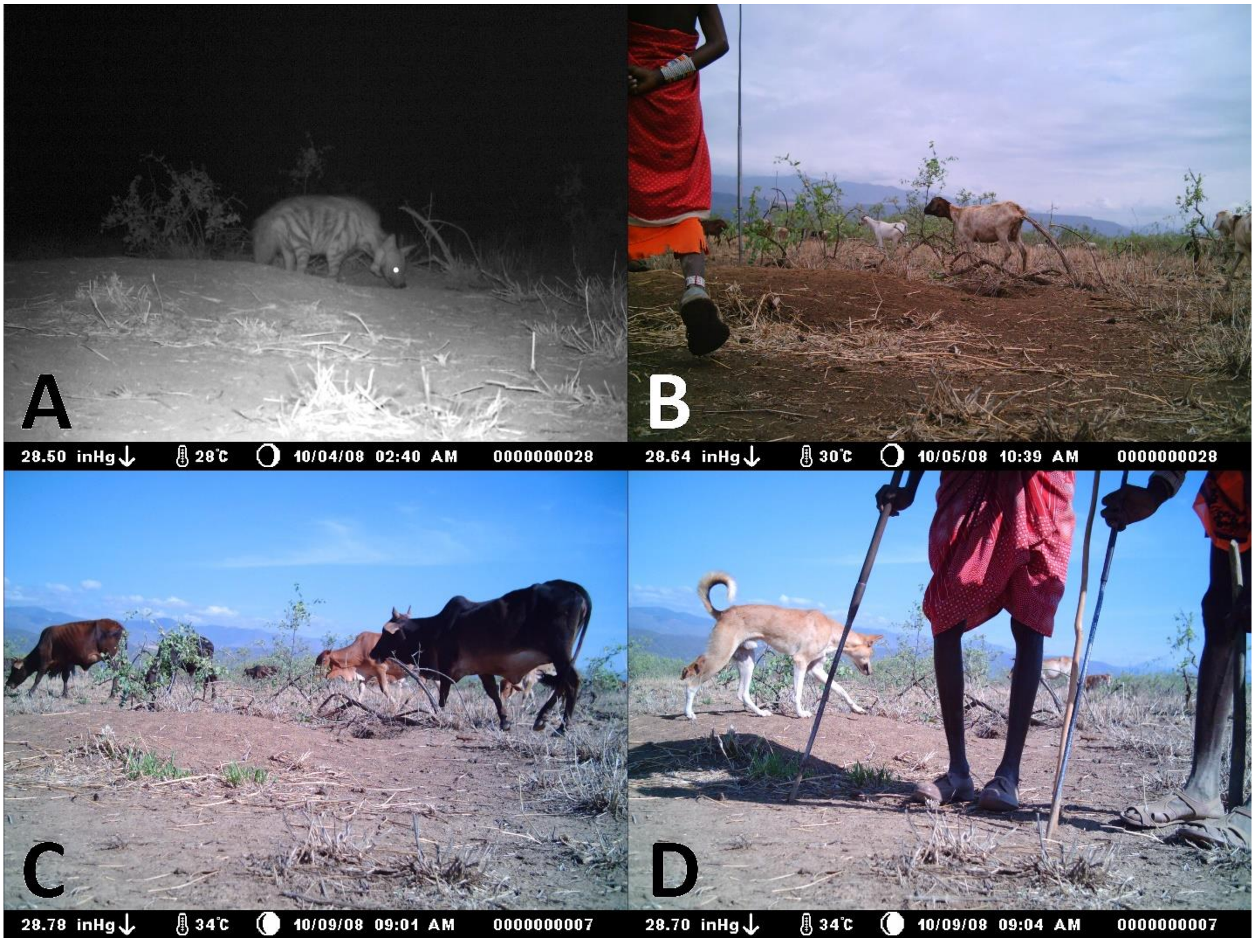
In Chapter Five, I expand upon our knowledge of social behavior in the least understood extant hyaenid, the striped hyena, by assessing potential functions of their olfactory communication. Specifically, I conducted the first study to date of scent-marking in wild striped hyenas. This study took place on the Olkiramatian and Shompole Maasai group ranches in southern Kenya, where high densities of lions, striped hyenas, and livestock share a landscape (Figure 1.1). Although territorial demarcation has been presumed to be the primary function of scent-marking in this species, we found no support for this in our study population. Instead, we found strong evidence that hyenas scent-marked to advertise their presence to conspecifics (Wolff et al. 2002), with the highest rates of pasting observed when hyenas were traveling and when at sites likely to be visited by multiple conspecifics, such as home range junctions and large carcasses. Hyenas in this population showed extensive overlap in home range between closely related females (Califf et al. 2020), and one pair of female kin exhibited the first known cases of den-sharing and allonursing ever reported in this species. The social system observed in this population is quite different from that of a population in a resource-poor region of central Kenya, where hyenas persisted at a lower density and females only permitted males within their territories (Wagner et al. 2008, Califf et al. 2020). Thus, striped hyenas show great behavioral plasticity in response to ecological conditions and can be much more social than previously thought, even exhibiting cooperative care of offspring (Tichon et al. 2020, Hadad et al. 2023). Understanding ecological predictors of social grouping in striped hyenas should facilitate more accurate estimation of density across ecological gradients, leading to more accurate global and local conservation statuses (Akçakaya et al. 2006) and help us predict how their populations may respond to continued habitat fragmentation and loss, human activity, and climate change (Singh 2008, Gall et al. 2022).

Throughout my dissertation, I employed a range of methodological approaches to advance our understanding of the spatial ecology of large carnivores in human-dominated landscapes. Protected areas have long been the cornerstone of large carnivore conservation, but protected areas alone cannot prevent the decline of biodiversity (Di Minin et al. 2016, Kideghesho & Rija 2018, Connolly et al. 2021), necessitating the study and implementation of methods for human-carnivore coexistence beyond protected areas. My dissertation provides novel methodology for ecological monitoring, advances our knowledge of how human activity affects the behavior of threatened carnivores inside of protected areas, and provides directions for future research into human-carnivore coexistence in agricultural landscapes.

FIGURES

Figure 1.1

Striped hyenas are highly nocturnal, and many of the striped hyena dens we observed were exposed to frequent human disturbance during the daytime. Our images of this active den show presence of the mother of the den-dependent cub (a) and Maasai herders with sheep and goats (b), cattle (c-d), and a domestic dog (d) within a single week.



CHAPTER 2:

MAPPING KENYAN GRASSLAND HEIGHTS ACROSS LARGE SPATIAL SCALES WITH COMBINED OPTICAL AND RADAR SATELLITE IMAGERY

ABSTRACT

Grassland monitoring can be challenging because it is time-consuming and expensive to measure grass condition at large spatial scales. Remote sensing offers a time- and cost-effective method for mapping and monitoring grassland condition at both large spatial extents and fine temporal resolutions. Combinations of remotely sensed optical and radar imagery are particularly promising because together they can measure differences in moisture, structure, and reflectance among land cover types. We combined multi-date radar (PALSAR-2 and Sentinel-1) and optical (Sentinel-2) imagery with field data and visual interpretation of aerial imagery to classify land cover in the Masai Mara National Reserve, Kenya using machine learning (Random Forests). This study area comprises a diverse array of land cover types and changes over time due to seasonal changes in precipitation, seasonal movements of large herds of resident and migratory ungulates, fires, and livestock grazing. We classified twelve land cover types with user’s and producer’s accuracies ranging from 66%–100% and an overall accuracy of 86%. These methods were able to distinguish among short, medium, and tall grass cover at user’s accuracies of 83%, 82%, and 85%, respectively. By yielding a highly accurate, fine-resolution map that distinguishes among grasses of different heights, this work not only outlines a viable method for future grassland mapping efforts but also will help inform local management decisions and research in the Masai Mara National Reserve.

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Kenyan grassland heights across large spatial scales with combined optical and radar satellite imagery. *Remote Sensing 12*(7):1086.

INTRODUCTION

Grasslands represent one of the Earth's most common vegetation types (Lieth 1978, O'Mara 2012), covering nearly a fifth of the planet's land (Scurlock & Hall 1998) and providing important ecological, economic, and cultural services. They are responsible for an estimated 16%–17% of global primary production (Bazilevich & Rodin 1971, Whittaker & Likens 1975, Lauenroth 1979), serve as hotspots for floral and faunal biodiversity (Bond & Parr 2010, Boval & Dixon 2012), support endemic species (Bond & Parr 2010, Boval & Dixon 2012, Mayle et al. 2007), affect runoff and water quality (Hopkins & Holz 2006), and contain up to 30% of the Earth's total soil carbon, thus reducing greenhouse gas emissions (O'Mara 2012, Boval & Dixon 2012). Grasslands are critical to the maintenance of human economies, livelihoods, and cultures, particularly for low-income and marginalized peoples (Boval & Dixon 2012, Gerosa & Skoet 2009). In 2006, the area allocated for livestock grazing covered a quarter of the Earth's ice-free land (Steinfeld et al. 2006). By supporting livestock, grasslands allow people to produce high-protein food, such as meat and milk (Boval & Dixon 2012), in addition to creating employment opportunities and generating income (Gerosa & Skoet 2009). In recent decades, grasslands have suffered severe and increasing degradation; between 2000 and 2010, approximately half of global grassland ecosystems underwent degradation, due primarily to climate change and human activities (Gang et al. 2014).

The importance of grasslands, paired with their vulnerability to climate change and human activity, makes their management a high priority. However, monitoring and managing grasslands is challenging. Field surveys of grass condition and production are costly and difficult to implement at the scale of large grasslands (Pickup et al. 1994, Reeves et al. 2001, Tueller 2001, Wessman et al. 1997). Remote sensing has great potential for improving grassland monitoring. While traditionally underutilized, remotely sensed data have been employed in several recent studies to detect grass cover, biomass, and height in temperate to hyper-arid grazing ecosystems (e.g., Wessman et al. 1997, Saltz et al. 1999, Harris & Asner 2003, Schino et al. 2003, Marsett et al. 2006, Numata et al. 2007, Ferreira et al. 2013, Wang et al. 2013, Cimbelli & Vitale 2017). The studies cited here primarily used vegetation indices and fractions derived from data from passive, optical sensors, most commonly Landsat TM, to investigate correlates of spectral signatures with biophysical properties of grass, particularly biomass. Marsett et al. (2006), Numata et al. (2007), and Cimbelli and Vitale (2017) specifically focused on predicting grass height, using Landsat (Marsett et al. 2006, Numata et al. 2007) or Landsat and Sentinel (Cimbelli & Vitale 2017) data to explain up to 80% of variation in grass height (Marsett et al. 2006). Only two of the studies cited here (Wang et al. 2013, Cimbelli & Vitale 2017) used radar data in their analyses. Wang et al. (2013) combined multitemporal optical data with multitemporal radar data collected in the X-band, C-band, and L-band; they described correlations between data collected via different sensors but did not incorporate field data on land cover. More recently, Cimbelli and Vitale (2017) combined Landsat and Sentinel imagery with field data to predict grass height at medium resolution, but with limited success.

Although previous work suggests that remote sensing may be applicable to grassland management, several gaps in our current capabilities are apparent. First, most efforts to map grasslands fail to exploit the benefits of optical and radar sensor fusion. Second, most of the studies to date have been conducted using highly homogenous grasslands, such as pastures and prairies (Wessman et al. 1997, Harris & Asner 2003, Numata et al. 2007, Ferreira et al. 2013, Wang et al. 2013). Saltz et al. (1999), Schino et al. (2003), Marsett et al. (2006), and Cimbelli and Vitale (2017), on the other hand, used spatially heterogeneous study sites, but with varying success in characterizing the biophysical properties of grass. The mapping algorithm applied to the most heterogeneous of the landscapes (a hyper-arid erosional cirque in Israel; Saltz et al. 1999) performed particularly poorly at characterizing plant cover.

Here, we seek to build upon previous work by extending the use of remote sensing in estimating land cover to include differentiation of discrete grass height classes in a dynamic savanna landscape representing a mosaic of open grasslands, shrubs, riverine forests, and wetlands. By integrating optical and radar imagery with a large field dataset, we aimed to produce a current and accurate land cover map of the Masai Mara National Reserve (henceforth, "the Reserve") in southwestern Kenya. This work is unique in three important ways. First, we aim to differentiate among grasses of different heights, which represent an important component of habitat suitability for various animals (e.g., large herbivores; Bell 1971), among other diverse land cover types in a heterogeneous landscape. Second, our methods apply a novel fusion of sensor imagery to the classification of land cover within a grassland ecosystem: PALSAR-2 radar imagery, Sentinel-1 radar imagery, and Sentinel-2 optical imagery. Third, our resulting land cover map provides a highly accurate, detailed, and novel map of a region that is of utmost conservation priority because it comprises the natural habitat of an enormously diverse fauna.

BACKGROUND

We employed a combination of multi-date radar (PALSAR-2 and Sentinel-1) imagery and single date optical (Sentinel-2) imagery. Optical sensors are "passive," meaning they measure light (visible and infrared) emitted by the sun that has reflected off the Earth's surface. Synthetic aperture radar (SAR) sensors, on the other hand, are "active," meaning that they emit microwave energy and measure its backscatter from the Earth's surface (Bourgeau-Chavez et al. 2013). Microwave energy, unlike visible and infrared light, penetrates cloud cover, affording radar sensors "all-weather" capability (Bourgeau-Chavez et al. 2016).

SAR imagery has been described as a perfect complement to optical imagery for several reasons (Wang et al. 2013). First, as active sensors, SAR sensors can collect data at nighttime (Bourgeau-Chavez et al. 2013) and are not impeded by cloud cover. Second, radar and optical sensors collect data in different, complementary bands of electromagnetic energy. Unlike reflected light measured by optical sensors, SAR backscatter is affected by standing water, soil inundation, surface roughness, and plant structure, biomass, and moisture content (Wang et al. 2013, Bourgeau-Chavez et al. 2013, Zhu et al. 2012, Bourgeau-Chavez et al. 2009).

SAR sensors emit and detect microwave energy in the L-band (longest wavelength, lowest frequency), C-band, or X-band (shortest wavelength, highest frequency). The PALSAR-2 sensor measures backscatter in the L-band, meaning that it penetrates vegetative canopy and thus is sensitive to soil background, soil moisture, and standing water (Bell 1971, Bourgeau-Chavez et al. 2015). Co-polarized PALSAR-2 imagery is particularly useful for detection (Bourgeau-Chavez et al. 2009) and differentiation of wetland classes due to an enhanced double bounce effect from water surface and tree trunks (Bourgeau-Chavez et al. 2015). Cross-polarized PALSAR-2 imagery, on the other hand, is sensitive to biomass, making it useful for distinction of woody from herbaceous vegetation (Ramsey 1998). The Sentinel-1 sensor measures backscatter in the C-band and provides information about vegetation structure and texture (Mayaux et al. 2002).

METHODS

Study area

The Reserve (1510 km^2; Allen et al. 2019) constitutes the northernmost portion of the Serengeti-Mara ecosystem. The Reserve consists primarily of open, rolling grassland with small patches of riparian vegetation along rivers and seasonal watercourses. Rainfall occurs bimodally, with most rain falling November–December and March–May (Ogutu et al. 2008). The Reserve is bounded by the Oloololo Escarpment to the west and the Serengeti National Park to the south and is bisected north to south by the Mara River. The area west of the Mara River, known as the Mara Triangle, is managed by the Mara Conservancy, whereas the land east of the Mara River is managed by the Narok County Government. Due to differences in management, human disturbance, particularly livestock grazing, has been prevalent on the eastern side of the park in recent decades, whereas it rarely occurs on the western side.

In 2013, the Serengeti-Mara ecosystem was identified as one of only four remaining strongholds for carnivore conservation in East Africa (Riggio et al. 2013). It also seasonally hosts large herds of zebras and wildebeest migrating north from the Serengeti National Park (Sinclair & Norton-Griffiths 1979) and southwest from the Loita Plains (Stelfox et al. 1986), and it is inhabited by many species of resident herbivores as well (Sinclair & Norton-Griffiths 1979). Altogether, the Masai Mara National Reserve supports 25% of Kenya's wildlife, based on estimates from the 1990s (Western et al. 2009).

Remote sensing data

We combined multi-date imagery from the PALSAR-2, Sentinel-1, and Sentinel-2 sensors. Image dates were selected to be coincident with field data collection described in Section 3.3 below. All imagery was projected to the WGS 1984 Universal Transverse Mercator coordinate system, zone 36S. Images were stacked and clipped to the geometry of the Reserve boundary.

Radar imagery was collected by the PALSAR-2 sensor onboard the Advanced Land Observing Satellite 2 (ALOS-2) platform. PALSAR-2 (L-band, ~23 cm wavelength) images were recorded in Fine Beam Dual (FBD) mode, meaning that the sensor transmitted the signals horizontally and received hem both horizontally (HH, known as co-polarization) and vertically (HV, known as cross-polarization). These data were collected at high resolution (10 × 10 m).

PALSAR-2 imagery was captured on two dates, 18 May 2018 and 13 July 2018. The imagery was collected in ascending orbit at 28.6◦ (all incident angles given apply at the center of the scene but vary across the extent of the scene). Only one frame was required to cover the entire extent of the study area. Images were calibrated to sigma-naught. We used a 3 × 3 median filter to account for speckle, the coherent addition of backscatter from multiple scatterers in the same resolution cell, which is inherent to all SAR imagery (Bourgeau-Chavex et al. 2013, 2016).

Additional radar imagery was collected by the Sentinel-1 satellite constellation, operated by the European Space Agency (ESA). Sentinel-1 (C-band, ~5.5 cm wavelength) images were obtained in dual-polarization mode, meaning that signals were transmitted vertically and received both vertically (VV) and horizontally (VH). These data were collected in high-resolution mode (10 × 10 m).

Owing to the seasonal variation in the herbivore community composition, herbivore density, and rainfall, the Reserve is highly dynamic and surface features such as soil inundation and vegetative cover often change rapidly within a year. Therefore, it was critical to obtain satellite imagery and field data that were collected during the same time period. This guided our selection of Sentinel-1 data as the complement to the PALSAR-2 imagery. Sentinel-1 imagery was captured on two dates, 7 June 2018 and 19 June 2018. The imagery was collected in ascending orbit at an incident angle of ~33◦. One frame was sufficient to cover the entire study area. Images were calibrated to sigma-naught and filtered using a 3 × 3 median filter.

Optical imagery was collected by the Sentinel-2B satellite, also operated by the ESA. Sentinel-2 data are collected in 13 spectral bands, ranging from ~443 nm– ~2190 nm. One frame of Sentinel-2 Level-1C top-of-atmosphere reflectance imagery was acquired for a single date, 11 June 2018. We planned to use imagery captured in July 2018 in order to include optical data coincident with the 13 July PALSAR-2 data, but an image collected early in the month was obscured by cloud cover, and subsequent image captures were collected while prescribed burns were occurring within the Reserve. We did not include the burned optical imagery in our analysis as our SAR imagery was collected before the burns, and our field verified sites did not include any already burned areas. Burned grasslands can experience enhanced regrowth and typically recover very rapidly. The visible and near-infrared bands (collected at 10 m resolution) along with vegetation red edge and shortwave infrared bands (collected at 20 m resolution) were used in this study. The bands collected at 20 m resolution were resampled to 10 m resolution using a nearest neighbor technique.

Training and validation data

Field data were collected throughout the Reserve between 4 June and 28 July 2018 to generate a supervised dataset for land cover classification. This time period did not overlap with either of the two rainy seasons and occurred prior to the arrival of the migratory herds of large herbivores. Therefore, grass height is unlikely to have changed substantially over the 54-day period of data collection. Our goal was to identify a minimum of six locations per land cover class (see Table 2.1 for definitions of land cover classes considered) to allow for a minimum of four training data and two validation data per class. We based our operations at the two field sites of the Mara Hyena Project (UTM coordinates: 751839 E, 9837939 N, and 724390 E, 9845214 N), and we therefore primarily collected data within the study areas monitored by the Mara Hyena Project. Specifically, we used ESRI ArcGIS to randomly generate 150 locations in the territories of three different hyena clans, covering a total of 71 km^2 west of the Mara River and a 61 km^2 area east of the Mara River. Random selection of locations was inefficient at identifying rare land cover classes, such as wetlands, water, barren ground, and *Acacia*-studded grassland (henceforth, shortened to “grass *Acacia*”). Therefore, we supplemented our field data by opportunistically sampling these rare land cover types when we encountered them in the field (this was also done by Bourgeau-Chavez et al. 2013).

At each field location, GPS (model: Garmin GPSMAP 78) coordinates were recorded using the averaging feature to improve horizontal accuracy and geotagged photographs were taken in the four cardinal directions and at nadir. For each sample area, we recorded the extent of the sample area, the land cover class, the dominant vegetation type, the approximate average height of the dominant vegetation, the percentage of vegetative cover, the distribution of the vegetation (homogeneous, heterogeneous, or patchy), and water inundation of the soil.

We collected field data at 233 locations. Polygons representing field data were hand-digitized using Google Earth Pro. Each polygon was drawn to include the GPS coordinates collected in the field. In some cases, these polygons were later reshaped to increase homogeneity within polygons to circumvent problems induced by spatial misalignment between sensors (Figure 2.1) and to avoid mixed pixel effects in dynamic areas. Some large original field site polygons were split to form two or more smaller, more homogeneous polygons in cases where the site was split by roads or the Mara River. A small number of polygons were deemed poor quality (e.g., not representative of a single land cover type, too heterogeneous) or were too small to avoid problems caused by mixed pixels or sensor misalignment and were therefore deleted. In total, we used 190 polygons based upon field observations. Of the field-derived training polygons, 136 were used for training and 54 were reserved for validation. Additionally, we added polygons for rare but easily detectable classes (e.g., water) from photo interpretation using both aerial imagery and our multi-sensor composite stack imagery; these points were not visited in the field. A total of 113 polygons were added based on visual interpretation of imagery. Of the 113 polygons added, 32 (28%) were upland forest, 20 (18%) were water, 13 (12%) were riverine forest, 8 (7%) were grass *Balanites*, 4 (4%) were grass *Acacia*, and the remaining 36 (32%) were wet meadow, emergent wetland, shrub, and barren. A total of 303 training and validation polygons collectively covering approximately 3.5 km^2 were used for the final classification and validation (Table 2.2).

Supervised land cover classification

Land cover across the Reserve was classified using the process depicted in Figure 2.2. We first randomly partitioned our supervised data into two categories, a training set and a validation set. Polygons representing approximately 80% of the area for each class were included in the training set (Table 2.2), while polygons accounting for the remaining 20% were reserved as an independent validation set. Polygons representing sites that were visited during fieldwork were prioritized to be included in the validation dataset. Supervised data added via visual interpretation of aerial imagery but not verified via ground-truthing were only used as validation data in cases where the field verified polygons did not reach the 20% threshold. This was done to ensure that validation used field-verified data whenever possible. In the final classified map, only the upland forest class contained polygons that were used as validation but were not visited in the field.

The training dataset and imagery stack were used to predict land cover for each pixel in the study area using the machine learning algorithm Random Forests (Breiman 2001, Liaw & Wiener 2002) in R version 3.6.1 (R Core Team 2023). The training data were selected from the training data polygons by selecting 100 random pixels from each land The training dataset and imagery stack were used to predict land cover for each pixel in the study area using the machine learning algorithm Random Forests (Breiman 2001, Liaw & Wiener 2002) in R version 3.6.1 (R Core Team 2023). The training data were selected from the training data polygons by selecting 100 random pixels from each cover class. Random Forests uses both a random sample of the training data and a random subset of predictors (image bands) to create a decision tree that best classifies the data. This is repeated multiple times until a “forest” of decision trees is generated. Each decision tree generates a “vote” for the most likely land cover class for the given pixel, and the pixel is assigned to whichever land cover class receives the most votes. We used 500 trees in our classifier and used the default node size of one. The RandomForests classifier was deemed optimal for this study based on its high classification accuracy and relatively low processing time. Additional benefits of Random Forests include its insensitivity to missing data (Zhu et al. 2012), such as pixels obscured by cloud cover (Bourgeau-Chavex et al. 2015) and nonpredictive input data, its capability for classifying datasets with many variables and relatively few training data (Zhu et al. 2012, Liaw & Wiener 2002), and the fact that it is easy to use (Breiman 2001) and allows for parallel processing (Liaw & Wiener 2002).

After classification, the validation data were compared to the predictions of Random Forests to assess accuracy. The overall accuracy is the total number of correctly identified validation pixels divided by the total number of validation pixels. Within each land cover type, the producer's accuracy is the number of pixels correctly identified as the given land cover type divided by the total number of validation pixels of that class. In other words, we determined the percentage of pixels in a given class that were correctly identified. As producer's accuracy increases, omission error decreases. The user's accuracy is derived by dividing the number of pixels correctly identified as a given land cover type by the total number of pixels assigned to that class, whether they were correctly identified or not. In other words, for each given class, we determined the probability that a pixel identified as that class truly does belong to that class. User's accuracy, also known as reliability, increases as commission error decreases. Results are presented in an error, or confusion, matrix (Table 2.3). Our mapping goal was to achieve a minimum of 75% producer's and user's accuracies for each land cover type and an overall accuracy higher than 75%.

Based on the resultant map and confusion matrix, additional training polygons were added or removed via visual interpretation of high-resolution satellite imagery. A few field data had to be removedastheareaofthelandcoverwastoosmalltocovertheminimummappingarea. Field-verified polygons that had been mapped using aerial imagery to define boundaries had to be buffered inward to avoid having mixed pixels within the scale of our 10 m resolution imagery. Additional riverine and upland forest polygon classes had to be added with visual interpretation of aerial imagery. After revision, data were once again assigned to training or validation data sets (prioritizing field-verified polygons for validation), and the Random Forests algorithm was run again. We aggregated the *Croton* shrub and *Euclea* shrub classes into a single shrub class.

Between iterations of Random Forests, if a class received additional training data (i.e., from visual interpretation), then the polygons in that class were once again randomly split.

Therefore, for the classes requiring additional training polygons, validation data in the final classification may have been used in a prior run as training data. The most important classes of grass height were not affected, as we could not use visual interpretation. In the final classification iteration, we utilized a new image stack with different dates designed to avoid confusion with the burned areas. Given the change in predictor variables, we believe the final run can be considered independent of previous runs.

RESULTS

We combined a10 m resolution imagery stack (dual date PALSAR-2, dual date Sentinel-1, and single date Sentinel-2) with training and validation data to assign land cover of the Masai Mara National Reserve using a Random Forests classifier. The resultant map (Figure 2.3) had an overall accuracy of 86%. The producer's accuracies for individual land cover classes ranged from 75% to 100% and the user's accuracies ranged from 66% to 100% (Table 2.3). This map will be made publicly and freely available as a Tagged Image File Format, compatible with ArcGIS and QGIS, via the Michigan Tech Research Institute (Ann Arbor, MI, USA) website.

Recall that the producer's accuracy is the likelihood with which a validation pixel for a given class was correctly classified, whereas the user's accuracy is the likelihood that a pixel assigned to a given class truly represents that class. The highest class-level accuracy was obtained for water, such as permanent water holes and rivers, which had producer's and user's accuracies of 99% and100%, respectively. Most of the observed confusion occurred between riverine forest, upland forest, shrub, and grass *Acacia*, but this error was not substantial; this confusion increased class-level omission error by a maximum of 21% (riverine forest) and commission error by a maximum of 22% (shrub). Not surprisingly, medium grass had the lowest user's accuracy (82%) of the grass heights due to confusion between tall and short grasses. That is, slightly more confusion occurred between tall and medium grass and between medium and short grass, than between tall and short grass. The three grass height land covers were all identified with accuracies of 82% or higher, with accuracies as high as 85% (user's) and 88% (producer's) obtained (Table 2.3).

Variable importance of our image bands was quantified using the mean decrease in accuracy metric (Figure 2.4) (Liaw & Wiener 2002). We looked at the importance of all the image bands to the overall classification, and we also looked at the importance of bands to classifying the three grass height land cover types. Values represent the loss in out-of-bag classification accuracy for each input band if that band had been excluded or permutated. Cross-polarized backscatter from L-band PALSAR-2 collected on 13 July 2018 was the most important band for the full classification as well as for the grass classes individually. The cross-polarized component of radar backscatter is typically due to significant volume scattering and is especially sensitive to biomass, so the importance of the variable for discriminating grass height, shrub, and forest is not surprising. Sentinel-2 red edge bands were also important, which highlights the strength of those bands for distinguishing vegetation types. Of some interest is the relatively low importance of C-band Sentinel-1 data. Cimbelli and Vitale (2017) also found Sentinel-1 to have limited value in assessing grass height in a study region in Italy.

The most common land cover across the Reserve was tall grass (31.0%), followed by medium grass (19.7%). Short grass covered 10.19% of the study area, similar to grass *Acacia* (12.0%), grass *Balanites* (11.0%), and shrub (8.8%) (Table 2.4). Collectively, grass constituted 60.9% of the entire study area. The rarest classes were water (0.3%), followed by wetlands (1.3% emergent wetland and 1.1% wet meadow), and forests (1.1% riverine forest and 0.9% upland forest). Visual inspection of the map (Figure 2.3) corroborates our personal observations that upland forest primarily occurs along the Oloololo Escarpment, which runs along the western boundary of the Reserve, atop inselbergs, and sometimes on hills, particularly those with human settlements, including tourist lodges. Riverine forest is found along the Mara River, with some also appearing along the Talek River and other small rivers. Shrubs were over four times as widespread as riverine and upland forest combined. Also consistent with our personal observations, *Balanites* trees appeared to occur more densely west of the Mara River than east, specifically immediately east of the Oloololo Escarpment (Figure 2.3).

Wetlands occur infrequently throughout this habitat, comprising only 2.4% of the entire Reserve. Many of the existing wetlands (especially wet meadow) occurred west of the Mara River, in the Mara Triangle. This too is consistent with our personal observations.

DISCUSSION

Our land cover classification method proved highly effective in this heterogeneous and temporally dynamic ecosystem. Excitingly, this method was successful in differentiating grasses of different heights, which, to our knowledge, has not been previously achieved in such a diverse landscape mosaic. A mapping technique with this capability is particularly important for an area like the Masai Mara National Reserve, which is composed primarily of grasslands (83.8% of the area is covered by short, medium, and tall grass as well as grass *Acacia* and grass *Balanites*).

Visual inspection of our map (Figure 2.3) suggests several differences between the Mara Triangle (west of the Mara River), which is managed by the Mara Conservancy, and the portion of the Reserve managed by the Narok County government (east of the Mara River). Some of these differences may be due to differences in management, i.e., active vs. passive management of livestock grazing within the Reserve. Within the eastern side, progression from south to north (e.g., towards the northern boundary of the Reserve) coincides with a transition from tall to medium to short grass and sometimes to large patches of barren ground. That is, grasslands in this region appear to diminish with increasing proximity to the northern boundary. The southern boundary of the Reserve is the Kenyan/Tanzanian border, beyond which lies the Serengeti National Park. Beyond the northern boundary, on the other hand, some land is protected whereas other areas are not. For instance, the communities of Talek and N'Tipiliguani, which lie immediately north of the Reserve, have developed rapidly, leading to a fivefold increase in illegal livestock grazing in the park between 2008 and 2015 (Green et al. 2018, 2019). This could potentially explain the south–north transition in grass height and cover.

However, some differences in land cover between the western and eastern sides of the park are more likely attributable to naturally occurring topographic variation. For example, the Mara Triangle seems to contain higher proportions of wetlands than the rest of the Reserve. This may in part be attributed to the higher rainfall the Mara Triangle receives compared to the east side of the Reserve due to local precipitation patterns created by the Lake Victoria convergence zone (Norton-Griffiths et al. 1975). Additionally, the Mara Triangle is more densely populated by *Acacia* and *Balanites* trees than is the area east of the Mara River.

Although we consider this landscape to be a savanna–woodland mosaic, it is worth noting that grass is far more common than woody vegetation. Open grasslands constitute the majority of the entire Reserve (60.9%), followed by grasslands studded with sparse *Acacia* and *Balanites* (23.0%), and then shrubs (8.8%). Forests constitute only 2.0% of land cover within the Reserve. Historically, these grasslands have been maintained by frequent fire disturbance and uprooting of woody vegetation by elephants (Dublin et al. 1990). The frequent resetting of the successional clock by elephants and fires would explain why trees are less common than shrubs, which in turn are less common than grasses. Riverine forest is found primarily along rivers, particularly the

Mara River. Upland forest is primarily distributed along the top of the Oloololo Escarpment but is also commonly found atop inselbergs. Inselbergs, which are hills or small mountains that rise abruptly, typically consisting of granite or gneiss rock (Porembski et al. 1997; Figure 2.5), in the Reserve are typically topped by patches of shrubs or trees (Figure 2.6). Generally, the vegetation on inselbergs is distinct from that of the surrounding land cover due to harsh edaphic (i.e., amount of soil cover) and microclimatic (i.e., evaporation rate and degree of insolation) conditions (Porembski et al. 1997). Thus, inselbergs clearly contribute to the Reserve's diversity of land cover and vegetation types.

Although our overall and class-level accuracies were consistently high, the confusion between shrub and tree cover is worth mentioning. That is, riverine forest, upland forest, grass *Acacia*, and shrub were sometimes confused, resulting in a 5% decrease in the overall accuracy (Table 2.3). In future applications, the addition of lidar data (aerial or space-based) to measure vegetation height has great potential to help differentiate forests and shrubs and perhaps even grass heights. The inclusion of a texture metric might also resolve some of this confusion. Grass *Acacia* and grass *Balanites* are composed of flat grasslands with sparse tall trees and thus should be very rough-textured. Forests consist of trees (canopy layer) and shrubs (understory) of various heights, so they should also be somewhat rough in texture. Shrub patches, on the other hand, are relatively homogeneous in height and therefore should be relatively smooth in texture.

We hope that this map will prove useful for ecological research within the Reserve. The Reserve is home to a plethora of research projects, focusing on spotted hyenas (e.g., Strauss & Holekamp 2019b), lions (e.g., Elliot & Gopalaswamy 2017), cheetahs (e.g., Broekhuis et al. 2019), baboons (e.g., Grieneisen et al. 2019), Martial Eagles (e.g., Hatfield 2018), ungulates (e.g., Green et al. 2019), and river ecology (e.g., Schoelynck et al. 2019), to name a few. It should also be useful to managers in the Masai Mara. Overgrazing by livestock represents a serious and ongoing threat to this ecosystem. This map may inform management decisions by identifying large patches of barren ground or short grass, which may represent problem areas warranting allocation of management efforts. Furthermore, application of our methods using optical and radar imagery collected over time may represent a highly accurate, feasible, and cost-effective method for monitoring grassland condition.

These methods should also be applicable to other savanna–woodland landscapes in East Africa. They have proven effective, despite the spatially heterogeneous and temporally dynamic nature of this ecosystem. Furthermore, they are capable of differentiating short, medium, and tall grass. Open grasslands comprise well over half of this study area, so differentiating grass height is important for delivering a detailed, informative land cover map.

There are several notable advantages afforded by these methods. First, the combination of PALSAR-2, Sentinel-1, and Sentinel-2 yields data across a wider range of the electromagnetic spectrum [Bourgeau-Chavez et al. 2009, 2013, 2016, Zhu et al. 2012) than radar or optical imagery could separately, which provides more unique spectral signatures corresponding to different land cover types. The diversity of bands in which radiation is measured allows for inference about diverse features, from soil inundation to vegetation canopy structure (Bourgeau-Chavez et al. 2013, 2016). Second, the use of multidate data yields valuable information, particularly in a temporally dynamic landscape such as the Masai Mara National Reserve. For example, wet meadows are prone to seasonal drying, and therefore single-date imagery could falsely classify wet meadow as grassland or permanent water. Incorporation of imagery from a second date can reduce errors in classification of seasonally dynamic land cover classes. Third, the Random Forests classifier is well adapted for this application, due to its high classification accuracy, insensitivity to missing data [29], ability to function with relatively few training data (Zhu et al. 2012, Liaw & Wiener 2002), ease of use, and low processing time (Breiman 2001). Finally, using an independent validation data set allows for accuracy measurement and identification of sources of confusion.

Additional work is needed to incorporate the temporal effects of wildfire on grass heights. We know a portion of our map changed very rapidly during our field observation period due to fire. None of our field data were gathered after burning, but some training sites did burn after our field visits. Therefore, we chose to map the vegetation before the fire occurred, but it is of great importance to remember the product is a snapshot of conditions over a relatively short temporal period.

This method should also be applicable in classifying land cover in mixed grassland systems beyond East Africa. Remote sensing may represent a highly effective, logistically feasible, affordable method to monitor grassland conditions, which can inform effective management. The method developed and assessed in this paper demonstrates the utility of remotely sensed imagery in differentiating grass height, even within a spatially diverse and temporally dynamic ecosystem. Future work should seek to expand the application of this method to other mixed grassland ecosystems, explore imagery sources which are more accessible, and test the feasibility of developing algorithms that are not as heavily reliant on expensive field observations. If algorithms do require field data, it would be useful to determine how much data will be needed and for what temporal scales the maps are useful.

CONCLUSIONS

This study represents the first study to our knowledge to use remotely sensed data to accurately classify discrete classes of grass height among other diverse land cover types in a tropical savanna-woodland landscape mosaic, which is highly spatially heterogeneous and temporally dynamic. We combined multi-date radar imagery (PALSAR-2 and Sentinel-1) and optical imagery (Sentinel-2) from a single season with training data from ground-truthing (i.e., field data) and image interpretation to assign land cover at a fine spatial resolution (10 × 10 m) using a machine learning algorithm, Random Forests [40]. We reserved 20% of our supervised data for validation, allowing us to assess and report user's, producer's, and overall accuracy and subsequently add and refine supervised data to improve classification in an iterative process.

The resultant map was highly accurate, achieving user's and producer's accuracies ranging from 66%–100% and an overall map accuracy of 86%. In addition to classifying a wide variety of land cover types, from open water to forests, we were able to distinguish discrete grass heights (short, medium, and tall) with user's accuracies of 83%, 82%, and 85%, respectively. Furthermore, confusion between grassland and non-grassland land cover occurred at low rates of 1% (omission) and 4% (commission). Overall, most of the confusion in classification occurred between shrubs, forests, and grasslands dotted with Acacia trees or shrubs. However, confusion was still low.

We expect that this fine-resolution, highly accurate land cover map of an ecologically important protected area will inform wildlife managers and allow researchers to address new questions regarding habitat preference and land cover change over time. Furthermore, these methods can be repeated or expanded upon for implementation in other mixed grassland ecosystems.

TABLES

Table 2.1

Description of each land cover class mapped.

Class	Description
Barren	Exposed light soil (sand), red soil (murram), dark soil (black cotton), and/or rock. Light soil is often exposed along rivers or dry creek beds or in transitional areas. Red soil is often exposed in murram quarries, on roads and airstrip runways, and in transitional areas. Dark soil is often exposed in overgrazed areas.
Riverine forest	Characterized by broadleaf evergreen trees and dead forests along river/streams. Woody vegetation must have a minimum height of four meters.
Upland forest	Characterized by broadleaf evergreen trees and dead forests occurring away (e.g., upland) from river/streams. Woody vegetation must have a minimum height of four meters.
Grass *Acacia*	*Acacia*-studded grasslands. Grass is the dominant vegetation type, followed by shrubs/trees of the genus *Acacia*. *Acacia* crown closure constitutes a minimum of 10% cover.
Grass *Balanites*	*Balanites*-studded grasslands. Grass is the dominant vegetation type, followed by *Balanites* trees. *Balanites* crown closure constitutes a minimum of 10% cover.
Tall grass	Grass plains where grass is 75 centimeters in height or taller.
Medium grass	Grass plains where grass is between 30 and 75 centimeters in height.
Short grass	Grass plains where grass is 30 centimeters in height or shorter.
Shrub	Patches of shrubs, typically dominated by shrubs of the genera *Croton* or *Euclea*.
Water	Areas persistently inundated in water that do not typically show annual drying out or vegetation growth at or above the water's surface, such as streams, canals, rivers, lakes, estuaries, reservoirs, impoundments, and bays. Water depth is typically 0.5 meters or deeper, so surface and subsurface aquatic vegetation persistence is low.
Emergent wetland	Wetland characterized by emergent or floating vegetation, including lily pads, cattails, sedges, and rushes. Some submergent vegetation may occur as well. The water table is at or near the earth's surface. Seasonal drying is variable within this class of wetlands.
Wet meadow	Wetland characterized by primarily inundated grasses and sedges along with some cattails and rushes. Following monsoons, the water table is at or near the earth's surface. Seasonal inundation and or drying are common phenomena.

Table 2.2

Summary of supervised data. Field data (FD) polygons were visited in research vehicles, or ground truthed. 190 of the best (i.e., most homogeneous, largest) original 233 FD polygons were included in the final supervised dataset because. Polygons added via visual interpretation (VI) were not ground truthed, but rather were later identified via visual interpretation of remotely sensed imagery (i.e., PASLAR-2, Sentinel-1, and Sentinel-2) only.

	Polygons			Pixels	Area (m^2)
	FD	VI	Total	Total	Total
Barren	23	2	25	199	19,900
Riverine forest	10	2	12	205	20,500
Upland forest	5	17	22	209	20,900
Grass *Acacia*	7	0	7	201	20,100
Grass *Balanites*	10	8	18	199	19,900
Tall grass	31	0	31	203	20,300
Medium grass	37	0	37	217	21,700
Short grass	22	0	22	201	20,100
Shrub	24	3	27	202	20,200
Water	9	19	28	212	21,200
Emergent wetland	4	3	7	200	20,000
Wet meadow	8	3	11	197	19,700
Grand Total	190	57	247	2445	244,500

Table 2.3

Confusion (i.e., error) matrix of the Masai Mara National Reserve. Numbers represent pixels (10 x 10 m each). Numbers in gray cells represent pixels from validation dataset that were correctly identified by the Random Forests classifier.

Classified land cover	**True land cover**														
	Barren	**Riverine forest**	**Upland forest**	**Grass *Acacia***	**Grass *Balanites***	**Tall grass**	**Medium grass**	**Short grass**	**Shrub**	**Water**	**Emergent wetland**	**Wet meadow**	**Sum**	**Commission**	**User Acc.**
Barren	190	0	0	0	0	0	0	0	0	1	0	0	191	1%	99%
Riverine forest	0	152	22	0	0	0	0	0	1	0	6	0	181	16%	84%
Upland forest	0	22	167	0	0	0	0	0	2	0	0	0	191	13%	87%
Grass *Acacia*	0	1	0	182	6	4	0	0	40	0	2	10	245	26%	74%
Grass *Balanites*	0	0	0	0	192	2	0	0	0	0	0	0	194	1%	99%
Tall grass	0	0	0	0	1	154	8	4	3	0	0	2	172	10%	90%
Medium grass	0	0	0	0	0	30	204	38	0	0	0	0	272	25%	75%
Short grass	9	0	0	0	0	13	5	159	0	0	0	0	186	15%	85%
Shrub	0	22	20	0	0	0	0	0	155	0	32	0	229	32%	68%
Water	0	0	0	0	0	0	0	0	0	211	0	0	211	0%	100%
Emergent wetland	0	8	0	0	0	0	0	0	1	0	153	1	163	6%	94%
Wet meadow	0	0	0	19	0	0	0	0	0	0	7	184	210	12%	88%
Sum	199	205	209	201	199	203	217	201	202	212	200	197			
Omission	5%	26%	20%	9%	4%	24%	6%	21%	23%	0%	24%	7%			
Prod. Acc.	95%	74%	80%	91%	96%	76%	94%	79%	77%	100%	77%	93%			**86%**

FIGURES

Figure 2.1

Great care had to be taken in delineating supervised data (polygons) to account for spatial misalignment of data collected by different sensors. Here, a patch of *Euclea* shrubs is shown using (a) Sentinel-2 band 4 (image captured 11 July 2018) and (b) Sentinel-1cross-polarization (VH; image captured 13 July 2018). We aimed to limit the polygons to pixels where the patch, or feature, of interest, as shown by each sensor, overlapped.

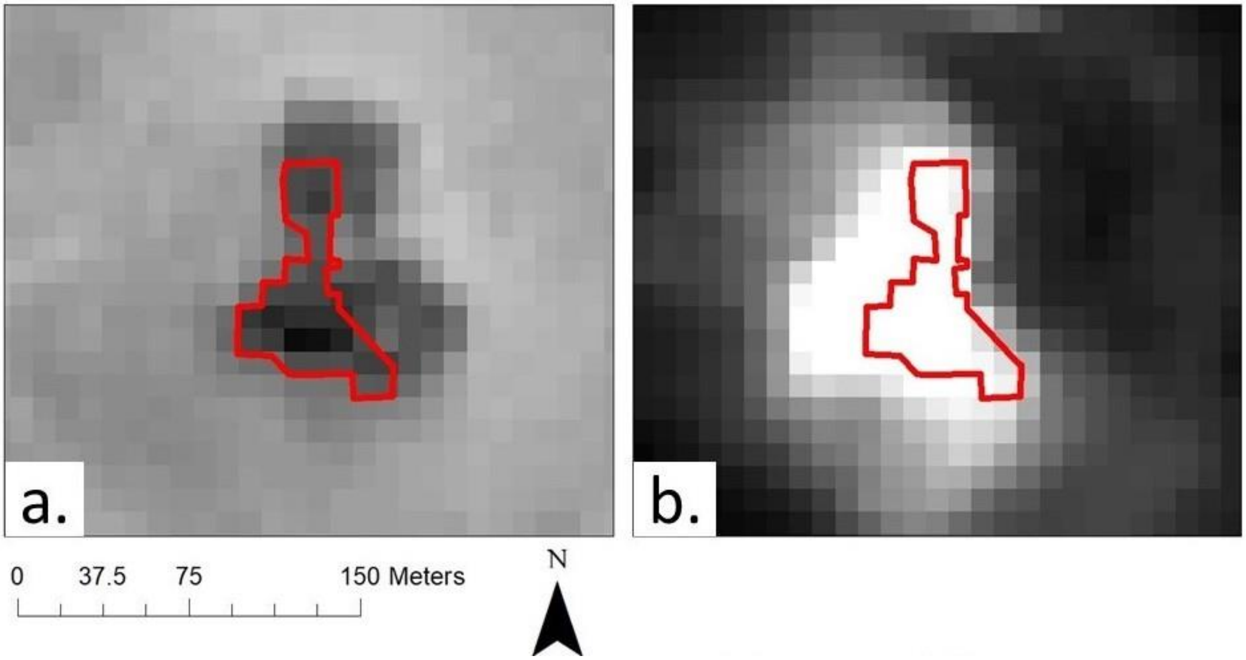


Figure 2.2

An overview of the land cover classification process. We reserved 20% of the polygons from the supervised dataset for validation, prioritizing field-verified sites. These validation polygons were not used in creating the Random Forests classifier. The other 80% of the supervised data and the multi-sensor composite stack imagery were input into a Random Forests classifier. The validation data were then used to construct a confusion matrix to assess accuracy. Visual inspection of the resultant land cover map and the confusion matrix informed subsequent refinement, addition, and deletion of supervised data and combination of classes.

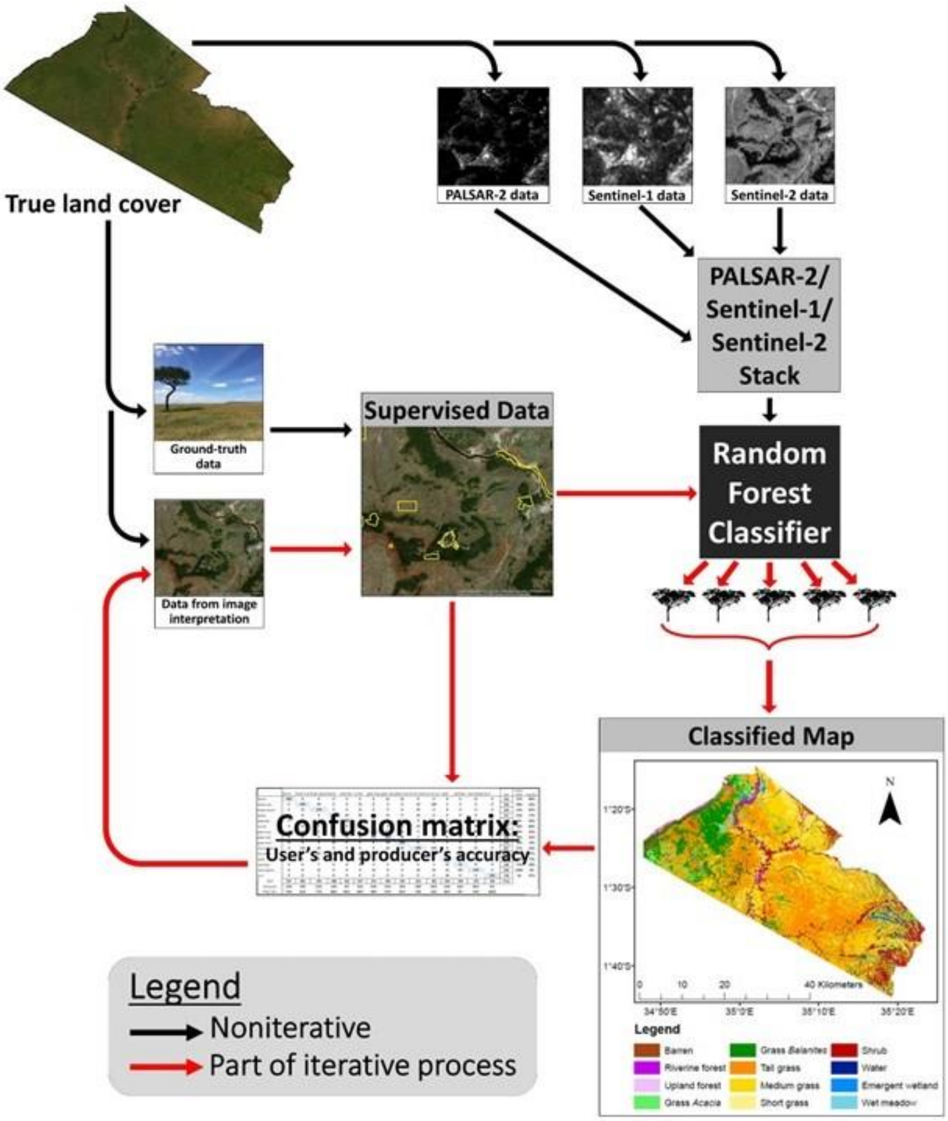


Figure 2.3

Land cover map of the Masai Mara National Reserve, with an overall accuracy of 86%.

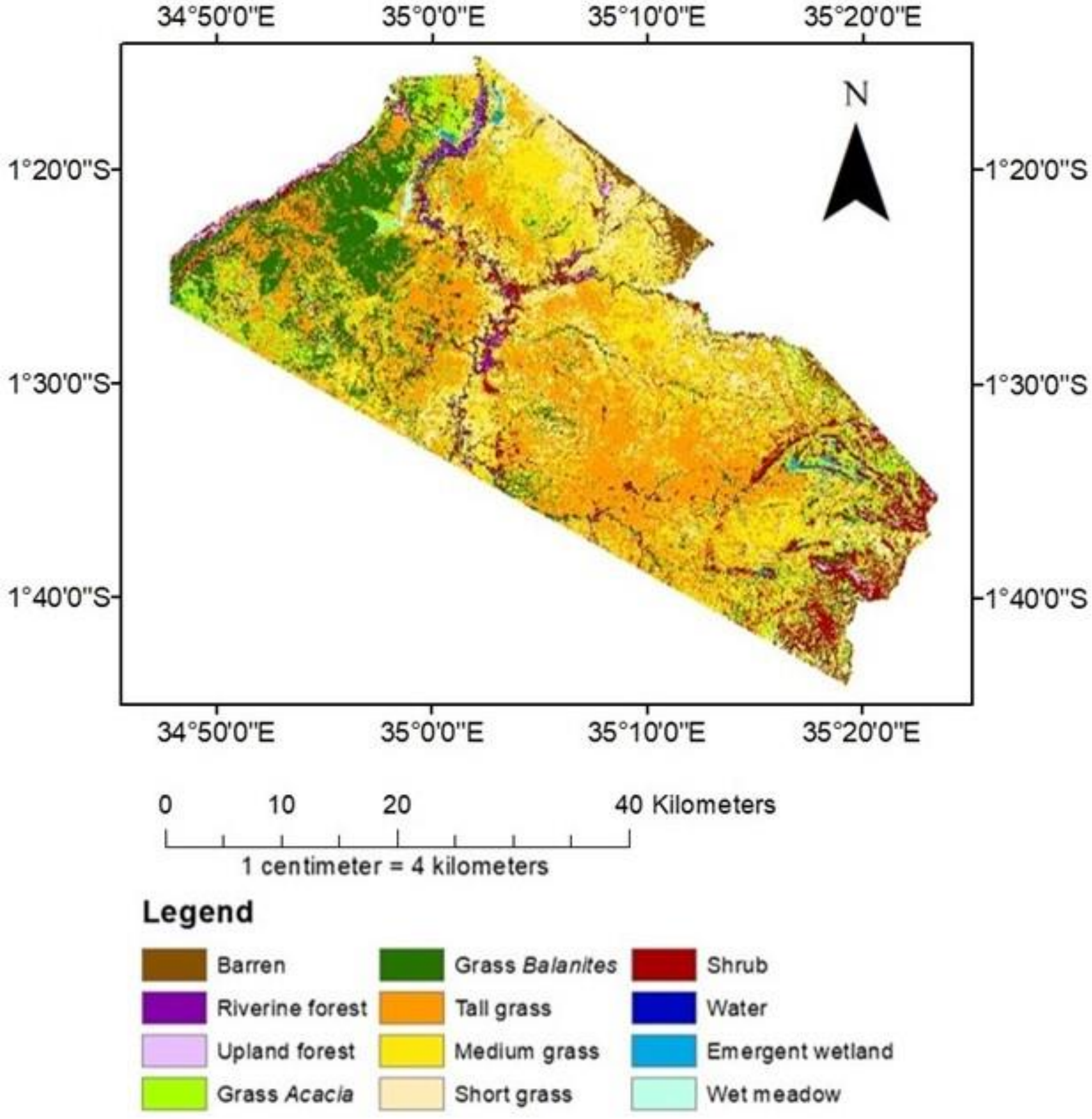


Figure 2.4

Mean Decrease Accuracy for all classes (black), short grass (green), medium grass (yellow), and tall grass (blue).

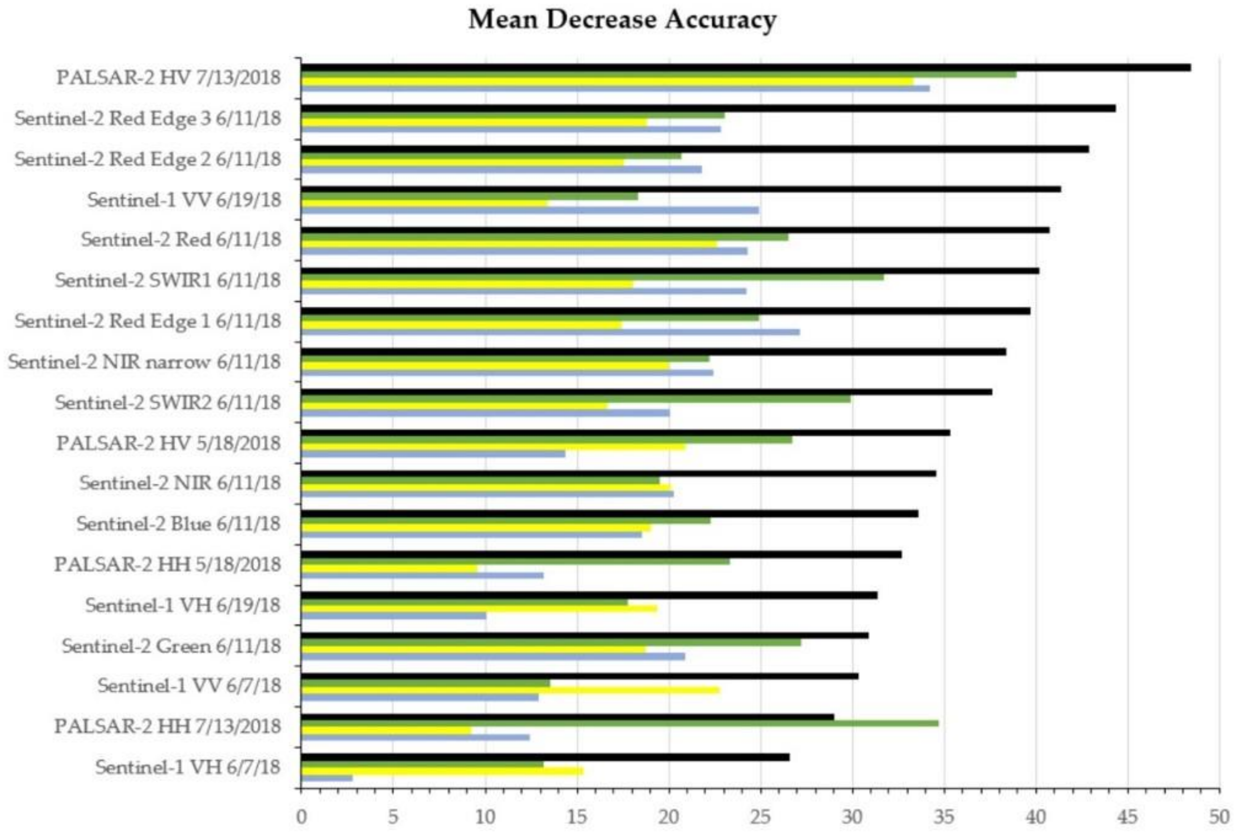
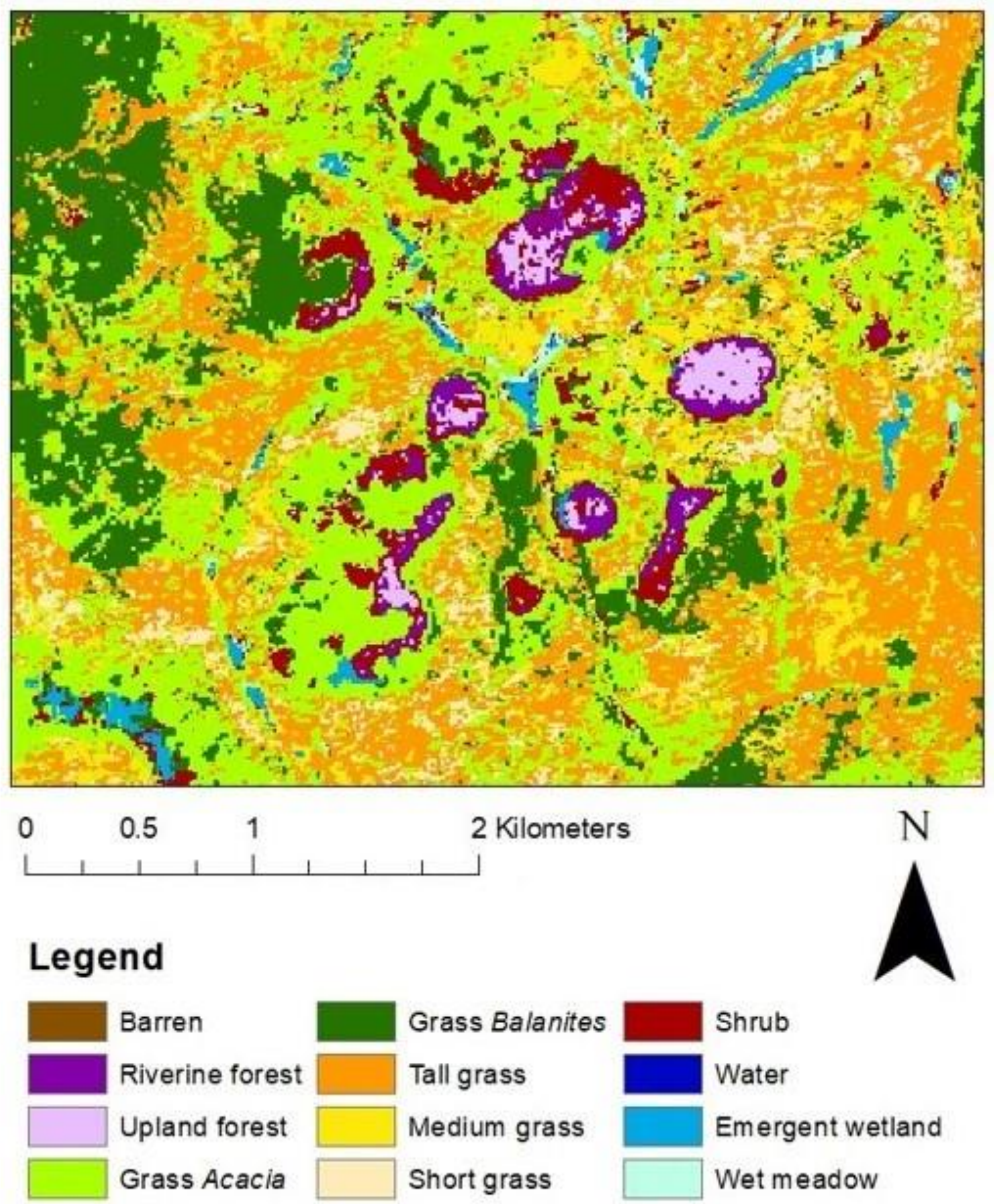


Figure 2.5

Inselbergs typically occur as abruptly rising, solitary, monolithic hills or mountains. They are particularly common in the tropics and subtropics (Porembski et al. 1997). This photo was taken in the southern Mara Triangle, where inselbergs are quite common.

Figure 2.6

A cluster of inselbergs in the southwestern Mara Triangle, on which rock and dense woody vegetation occur.



CHAPTER 3:

EFFECTS OF LIVESTOCK ABUNDANCE ON SPACE USE BY LIONS, CHEETAHS, AND BLACK-BACKED JACKALS IN THE MAASAI MARA NATIONAL RESERVE, KENYA

ABSTRACT

Human activity has had catastrophic effects on global populations of large carnivores. Large carnivores play important ecological roles, and both population reductions and behavioral changes can have tremendous effects throughout the rest of the ecosystem. Among the top global threats to large carnivores is conflict with humans, which represents a primary source of mortality even in many protected areas. We sought to determine how livestock grazing inside of a protected area in Kenya affected space use by native carnivores. We recorded the spatial distribution of large carnivores in the Maasai Mara National Reserve over a period of several years during which the intensity of livestock grazing fluctuated widely. We investigated how the livestock abundance affected the use of vegetative cover and the distance to the Reserve boundary of lions, cheetahs, and black-backed jackals. We also examined how herders and livestock may mediate mechanisms of coexistence within the carnivore community. Effects of livestock abundance varied by carnivore species and were strongest for lions. As livestock abundance increased, we saw fewer lions during daytime, especially near the Reserve boundary, which was used intensely by livestock. This is likely because of the high persecution of lions by local people. Carnivore conservation is likely to increasingly rely on humans' ability to share space with them, especially in agricultural landscapes. We encourage prioritization of research into how pastoralists can spatially and temporally partition resources with carnivores and implementation of findings into livestock management.

INTRODUCTION

Large carnivores are of great ecological, socioeconomic, and intrinsic value. They are critical for maintaining ecosystem structure, function, and resiliency, and their extirpation, reductions in their abundance, and even shifts in their behavior often result in a trophic cascade – a progression of indirect top-down effects on species interactions (Ripple et al. 2016) – that can have enormous effects on sympatric populations of scavengers, mesopredators, prey, and plants through altered trophic interactions. These top-down effects can even alter processes underlying disease outbreaks, invasion by nonnative species, wildfires, and carbon sequestration, as well as the composition of soil, water, and the atmosphere (Ritchie et al. 2009, Estes et al. 2011, Ripple et al. 2014). By exerting control over mesopredator and herbivore populations, large carnivores can produce economic and public health benefits by reducing zoonotic disease transmission, agricultural losses, and vehicle-wildlife collisions (Prowse et al. 2015, Gilbert et al. 2017, Braczkowski et al. 2018, Thinley et al. 2018, Rode et al. 2021). They also create economic opportunities through tourism and hunting and hold cultural significance for many communities (Rode et al. 2021).

Despite their ecological and socioeconomic importance, large carnivores have become some of the world's most threatened taxa in the face of anthropogenic change (Estes et al. 2011, Ripple et al. 2014, Di Minin et al. 2016). Because of their high trophic position, they often require large home ranges, persist at low population densities, and have slow life histories. These characteristics render their populations ill-equipped to adapt to the rapidly-changing environmental conditions of an increasingly human-dominated global landscape (Ripple et al. 2014). They are also perceived to pose threats to human safety, livelihood, and recreation, resulting in low tolerance by humans (Ripple et al. 2014). Consequently, the majority of the world's largest carnivores are at risk of extinction and experience ongoing population decline and occupy less than half of their historical geographic ranges. Where they remain, many populations face severe habitat degradation and fragmentation (Ripple et al. 2014).

As co-occupants of the highest trophic levels, large carnivores and humans compete for resources such as food (livestock) and space, bringing them into frequent conflict (Treves & Karanth 2003). Human-carnivore conflict is continuously exacerbated by habitat loss, which forces large carnivores into increasingly close proximity to humans (Treves & Karanth 2003, Cardillo et al. 2004, Inskip & Zimmerman 2009, Ugarte et al. 2019), and is among the most prevalent threats to the survival of large carnivores (Ripple et al. 2014, Di Minin et al. 2016). Protected areas have long been considered the cornerstone for biodiversity conservation (Watson et al. 2014, Di Minin & Toivonen 2015), but they themselves are not immune to the pressures imposed by anthropogenic activity (Woodroffe & Ginsberg 1998, Balme et al. 2010); even in protected areas, persecution is usually the primary source of mortality for adult large carnivores (Broekhuis et al. 2019). Aside from direct mortality, humans may also induce behavioral changes in wildlife that bear energetic costs for carnivores (Boydston et al. 2003, Oriol-Cotterill et al. 2015b, Clinchy et al. 2016, Green & Holekamp 2019) or alter interactions between predators and prey (Boydston et al. 2003, Berger 2007, Smith et al. 2015), among carnivore species (Clinchy et al. 2016, Klaassen & Broekhuis 2018, Shores et al. 2019), or within carnivore populations (Støen et al. 2015).

Protected areas in East Africa are of monumental conservation importance, but some also face severe pressure from human activities, including poaching, tourism, and livestock production. The Mara-Serengeti is home to one of the few remaining intact large predator guilds in the world (Craft et al. 2015, Hampson et al. 2015) and is one of the last remaining refugia for large carnivore conservation in East Africa (Ogutu & Dublin 2002, Riggio et al. 2013). The northernmost portion of this ecosystem, the Maasai Mara, Kenya, serves as a multifunctional landscape and presents opportunities for conservation, tourism, and livestock production, leading to conflict among stakeholders with opposing interests (Butt 2014, Bedelian & Ogutu 2017). The seasonality of rainfall in this region requires the local people of the Maasai tribe to move their herds throughout the year to access seasonally variable grazing areas, which, for centuries, have included grasslands within the Maasai Mara National Reserve and the surrounding conservancies (Butt 2014, Bedelian & Ogutu 2017, Western 2018). During droughts, the grasslands contained within the boundaries of these protected areas are critical to the survival of the Maasai's cattle, and, in turn, the Maasai's economy, food security, and culture (Galaty 1982, Butt 2014, Chege et al. 2015, Bedelian & Ogutu 2017). Since the designation of these protected areas, the Maasai's access to historical grazing lands has been curtailed, and in the Reserve, it is legally prohibited (Butt 2014, Bedelian & Ogutu 2017). Effects of livestock grazing on ecosystems are highly variable and can be positive or negative (Niamir-Fuller et al. 2012), but high densities of livestock have been known to have devastating effects on native wildlife (Ogutu et al. 2016).

The intensity of livestock grazing exposure inside the Reserve has exhibited massive fluctuations both within (up to fivefold) and across years (over fiftyfold) as a result of human population expansion and changes in Reserve management. As the human population along the Reserve boundaries has rapidly grown, so too has the livestock population, causing considerable damage to the native herbivore community (Lamprey & Reid 2004, Reid et al. 2003, Green et al. 2018). In addition to these bottom-up effects on biodiversity, resulting from competition between livestock and domestic wildlife for access to food and water, a high density of livestock in the Reserve increases the prevalence of human-carnivore conflict, culminating in direct persecution of large carnivores (e.g., poisoning, spearing) that represents a primary source of mortality (Blackburn et al. 2016, Green et al. 2018) and creates a landscape of fear (Oriol-Cotterill et al. 2015a, Oriol-Cotterill et al. 2015b). Over the years, enforcement of cattle prohibition within the Reserve has been inconsistent and dependent on the current management (Green 2015, Green et al. 2018). A clear and sudden shift in the abundance and spatial distribution of native wildlife and vegetation soon followed, presenting a natural experiment through which the resiliency of this ecosystem could be investigated, but the recovery of this region has yet to be documented.

In addition to being a top priority for conservation, the Maasai Mara National Reserve is an ideal study system through which to illuminate the processes by which livestock grazing modifies the movement patterns of carnivores in a mixed-use landscape and how these effects may vary for dominant and subordinate carnivore species. Importantly, the wide fluctuations in livestock density inside the Reserve in recent years facilitate the treatment of livestock grazing intensity as a continuous variable, rather than simply binary (i.e., livestock present versus absent), as can be seen in earlier work on this topic in the Reserve (Boydston et al. 2003, Kolowski & Holekamp 2009, Green et al. 2018, Green & Holekamp 2019). A better understanding of the nuances of these interrelationships could inform management decisions aimed at maximizing the utility of protected areas for conservation (Rostro-García et al. 2015) while serving local economies through ecotourism and evidence-based livestock husbandry. Herein, we leveraged historical observational data to assess the effects of livestock density inside the Reserve on the space use of three native mammalian carnivores: African lions (*Panthera leo*), cheetahs (*Acinonyx jubatus*), and black-backed jackals (*Lupulella mesomelas*; henceforth "jackals"). Effects of pastoralist activity can impose various effects on different carnivore species and modify intraguild interactions (Green et al. 2018, Farr et al. 2019), so we selected these species to represent dominant and subordinate predators, apex and mesopredators, a range of body sizes, and varying rates of conflict with humans.

We investigate how livestock abundance broadly affected space use by large carnivores. Carnivore avoidance of areas of intense use by humans, such as livestock grazing, has been evidenced by a large body of literature across diverse carnivoran taxa (Kolowski & Holekamp 2009, Klaassen & Broekhuis 2018). Anthropogenic effects inside protected areas are often strongest near the edges of the protected area (Woodroffe & Ginsberg 1998). In our study area, livestock density was typically highest near the points of entry along the Reserve boundary and decreased with distance to the boundary because the herders return their animals to their corrals outside the Reserve when they are not actively being grazed inside the park (Holekamp, personal communication). Lions and spotted hyenas (*Crocuta crocuta*) have been known to move deeper into the Reserve, away from the border, in response to intensifying livestock grazing inside the Reserve (Green et al. 2018). If carnivores avoid livestock, we expect them to increase their distance to the Reserve boundary when livestock abundance is high. Alternatively, if carnivores are attracted to areas heavily used by livestock – for example, because livestock supplement food available during times of native prey scarcity (Wolf & Ripple 2016) – then we expect them to decrease their distance to the boundary with increasing livestock abundance (Table 3.1). Attraction to livestock herds increases the likelihood of a fatal conflict with humans, but if carnivores feed on livestock – either by hunting or scavenging – this could also provide short-term benefits.

Avoidance of livestock likely bears energetic costs by limiting resource access or increasing time and energy spent traveling (Boydston et al. 2003, Kolowski & Holekamp 2009, Oriol-Cotterill et al. 2015a, Green & Holekamp 2019). Indeed, Boydston et al. (2003) found that spotted hyenas avoided areas that hosted high densities of both native ungulates and livestock, suggesting that the perceived threat posed by humans reduced hyena foraging efficiency. The Reserve boundary is demarcated by the Talek River, meaning that avoiding the edge of the Reserve would impede carnivores' access to the largest (but not the only) permanent water source in the area. Access to permanent water sources can be expected to be especially important to carnivores during times of drought for two reasons: first, to access water to drink, and second, because prey must visit these sites frequently (Ogutu et al. 2014). Rather than avoiding disturbed areas on a large scale (distance-sensitive avoidance), carnivores may instead avoid encounters with humans and livestock on a microscale by switching their habitat selection (habitat-mediated avoidance; Sergio et al. 2007). That is, carnivores may use dense vegetative cover to conceal themselves in the presence of herders and livestock (Kolowski & Holekamp 2009). If carnivores increase their use of closed habitat in response to increased disturbance by herders and livestock, then we expect to see a positive interactive effect between livestock abundance and the proportion of closed habitat on carnivore sighting frequency (Table 3.1).

Furthermore, we investigate how pastoralist activity differentially affects the space use of apex and mesopredators (Moll et al. 2018, Shores et al. 2019, Searle et al. 2021, Rodriguez Curras et al. 2022, Seveque et al. 2022). Lions are most likely to be targeted for persecution by Maasai (Kissui 2008, Koziarski et al. 2016), so we expect livestock abundance to exert stronger effects on lions' space use than on that of cheetahs or jackals. Lions and cheetahs have been found to avoid areas highly disturbed by human activity (Green et al. 2018, Klaassen & Broekhuis 2018, Madsen & Broekhuis 2020), and mesocarnivores may perceive humans as greater threats than native apex predators (Clinchy et al. 2016, Zanette et al. 2023). If all three species respond similarly to the presence of livestock and herders – for example, because mesopredators perceive humans to pose a greater risk than other large carnivores – then we expect livestock abundance to have a similar effect on all three species' distance to the Reserve boundary and use of closed habitat (Table 3.1). Alternatively, competition and predation risk imposed by dominant carnivores may be perceived as greater threats than those posed by humans (Shores et al. 2019). Among these three species, a linear hierarchy exits in which lions are dominant to cheetahs, lions and cheetahs are dominant to jackals, and subordinate carnivores are known to be killed by those above them in this hierarchy (Swanson et al. 2016, Kamler et al. 2020a). Thus, mesocarnivores may avoid dominant carnivores by selecting marginal habitats (Durant 1998), such as those characterized by intense human use. Lions, cheetahs, and jackals may also differ in their propensity to feed on livestock. If subordinate predators' space use is affected more strongly by dominant carnivores than by human activity, then we expect to see the effect of livestock abundance on space use (distance to boundary or use of closed habitat) to vary in direction (positive/negative) across our focal carnivore species (Table 3.1). Understanding how these species vary in their behavioral responses is important for predicting how pastoralism could mediate sympatric carnivore species' ability to spatially partition their habitat. As human disturbance intensifies globally, native carnivores must navigate an increasingly complicated set of decisions, incorrect assessment of tradeoffs can bear heavy consequences for native carnivore populations (Northrup et al. 2012, Prugh et al. 2023).

METHODS

Study area

The Maasai Mara National Reserve, southwestern Kenya, is bounded by the Serengeti National Park, Tanzania, to the south, the Oloololo Escarpment to the west, and private conservancies to the north and east. The Reserve is primarily characterized by open grasslands, interspersed with riparian vegetation lining seasonal creeks and wetlands. Rainfall occurs during two wet seasons: the “short rains” (November-December) and the “long rains” (March-May; Ogutu et al. 2008). The Mara-Serengeti supports one of the world’s richest mammalian carnivore communities with at least 30 species (Craft et al. 2015), a diverse resident herbivore community (Green et al. 2019), a mass migration of over a million wildebeest (*Connochaetes taurinus*; Sinclair et al. 2008, Mtewele et al. 2023), and a booming ecotourism industry (Butt 2014, Larsen et al. 2020, Narok County 2023).

The Mara River runs north to south, dividing the Reserve into two independently-managed regions. We conducted our research in the Talek region of the eastern portion of the Reserve (53 km^2), which is managed by the Narok County Government. The Talek River marks the boundary between this region of the Reserve and an island of unprotected land immediately to the north. Here, the town of Talek and the surrounding lands are occupied by a rapidly expanding population of Maasai pastoralists, and the presence of domestic sheep and goats (*Ovis aries* and *Capra hircus*, respectively; henceforth, “shoats”) and cattle (*Bos taurus*) has become pervasive inside the Reserve. Livestock are herded into the Reserve daily, using specific crossing sites along the Talek River and shoats typically stay near the river, whereas cattle graze up to several kilometers into the Reserve (Boydston et al. 2003). Livestock herds are most commonly herded into the Reserve at sundown and herded back out around dawn. Livestock are accompanied by herders carrying weapons such as spears.

Data collection

From 2013 to 2019, we measured rainfall daily using a rain gauge at our basecamp, located immediately next to the Talek River. Twice monthly, three four-kilometer-long transects were run, during which all native ungulates (representing 12 species) within 100 meters were counted. Twice monthly, between 1600 and 2000 h, we systematically counted all cattle and shoats in the study area.

We drove one or two vehicles throughout the study area twice daily (0500-1000 h and 1600-2100 h) for the purpose of locating and observing the behavior of spotted hyenas. Observations started and ended at our basecamp, and the morning observations often started by driving to a known communal hyena den, and evening observations often ended by returning from a den. During these observation periods, all incidental sightings of lions, cheetahs, and jackals were recorded, including their location, the time of day, and the number of individuals present. We did not identify individual animals, so a single individual could be counted on multiple occasions. This was not problematic here, since we investigated space use, not demography. Since this sampling was not systematic, we controlled for observer effort; we recorded all routes driven (henceforth, "tracks") during this period, using GPS units (model: Garmin GPSMAP 78) mounted in each vehicle.

Data extraction

For each month-year from 2013 to 2019, we extracted the total precipitation (mm), the mean total number of native ungulates recorded on transects, and the mean number of cattle, shoats, and total livestock counted during livestock counts. These variables were not spatially explicit; one value applied to the entire study area for each month-year.

We applied a 400 x 400 m resolution fishnet grid to our entire study area. For each unique cell, we extracted the following data for each month-year: the distance from the cell centroid to the Reserve boundary; the proportion of closed vegetative land cover ("closed habitat" included forest and shrub land cover identified by Spagnuolo et al. 2020); the total number of lions, cheetahs, and jackals sighted within each cell; and the total length of tracks intersecting the cell (observer effort; Figure 3.1). These variables were spatially explicit, since we were able to extract cell-specific values for each. All data management, extraction, and analyses were performed in R version 4.3.2 (R Core Team 2023) through RStudio version 2023.12.0.369 (Posit Team 2023). We used the package ‘sf’ to handle spatial data in R (Pebesma 2018, Pebesma & Bivand 2023) and projected all spatial data using the WGS 84 UTM zone 36 South (EPSG 32736) coordinate system.

Statistical analyses

Using each unique sighting as one datum, regardless of group size, we compared the distances to the Reserve boundary among lions, cheetahs, and jackals using an ANOVA (“stats” package, R Core Team 2023; “multcomp” package, Hothorn et al. 2008). The numbers of lions, cheetahs, and jackals seen per cell per month-year were separately modeled with zero-inflated generalized linear mixed models with negative binomial distributions, using the package “glmmTMB” (Brooks et al. 2017, Magnusson et al. 2017). Each data point (one cell per one month-year) was only included if it met our minimum requirement for observer effort density (1000 m of tracks per cell). The original candidate model for each carnivore species included main effects of distance to Reserve boundary, proportion of closed habitat, livestock abundance, native ungulate abundance, and total precipitation; interactive effects of livestock abundance and distance to Reserve boundary, livestock abundance and proportion of closed habitat, and native ungulate abundance and distance to edge; an offset for observer effort; and a nested random effect of cell ID within month-year. Candidate models for cheetahs and jackals also included a main effect of the number of lions seen within each cell. To facilitate model convergence, precipitation was dropped from all models, and distance to Reserve boundary, livestock abundance, and native ungulate abundance were standardized.

RESULTS

Temporal trends in environmental variables

The seasonality and total amount of precipitation varied across years, but overall followed the expected seasonal distribution (Figure 3.2). During the mass migration (June-August), migratory herds of wildebeest and zebras enter the Reserve from the Serengeti. The Reserve also supports resident herds of these two species, among many others. From 2013 to 2019, the mean abundance of native ungulates was highest from June to August (Figure 3.3), mainly due to the massive influx of migratory wildebeest. The two migratory species plus Thompsons gazelles collectively composed 90.7% of all native ungulates seen on transects from June-August (migration), and 79.6% from September-May (non-migration). During both of these periods, the five most abundant species included Thomson’s gazelles, wildebeest, topi, zebras, and impala, while the remaining seven species accounted for less than 4%.

The mean total abundance of livestock counted within our study area was under 2,000 (37.7 animals/km^2) from April to November, climbed to 3878.4 ± 4119.3 (mean ± 95% confidence intervals) in March (73.2 animals/km^2), and abruptly dropped off with the arrival of the long rains in April (Figure 3.4). The highest mean abundances of livestock were observed in 2014 and 2015 (3763.7 ± 1521.3 and 4002.9 ± 2203.1, respectively), and mostly consisted of cattle, after which the mean abundance of cattle dropped from 2927.9 ± 2039.8 in 2015 to 440.8 ± 330.3 in 2016. In 2018, livestock abundance further dropped to 69.1 ± 48.9 (1.3 animals/km^2; Figure 3.5), the lowest livestock abundance this area has seen since the 20th century (Green et al. 2017).

Carnivore space use

Between 2013 and 2019, a total of 1,950 lions were sighted on 569 unique occasions. Mean group size was 3.43 (median two), and the largest group seen was a group of 16 (nine cubs, three subadults, and four adults). 994 cheetahs were sighted on 422 occasions, with mean and median group sizes of 2.36 and one, respectively. The largest group seen consisted of a mother and six dependent cubs. We sighted 5,074 jackals on 2,977 occasions, with a mean observed group size of 1.70 and a median of two. The largest group (eight jackals) was seen at a jackal den. Where each datum represents one cell/month-year for which sufficient observer effort was allocated, our final sample size was 5,928. Cheetahs maintained significantly greater distances to the boundary (mean ± std dev = 2456.445 ± 1461.562 m) than lions (1887.35 ± 1532.22 m, $p < 0.0001$) or jackals (1561.315 ± 1240.41 m, $p < 0.0001$), and lions maintained greater distances than jackals ($p < 0.0001$).

The strongest predictor of lions' space use was the proportion of closed habitat, which had a significant positive effect (5.49 ± 1.58, β ± std err, $p < 0.001$, Figure 3.6). Livestock abundance alone had a negative effect on lion counts across the entire study area (-0.74 ± 0.35, $p < 0.05$). More lions were seen with increasing distance to the Reserve boundary (i.e., deeper into the Reserve; 0.60 ± 0.16, $p < 0.001$, Figure 3.6), and this effect was further strengthened with increasing livestock abundance (0.62 ± 0.21, $p < 0.01$, Figure 3.7).

In contrast to lion sightings, the frequency of cheetah sightings was negatively correlated with the proportion of closed habitat (-4.44 ± 2.31, $p = 0.055$) and significantly positively correlated with livestock abundance (-1.05 ± 0.32, $p < 0.001$). Like lions, cheetahs' site-specific space use was positively predicted by distance from the Reserve boundary (0.60 ± 0.16, $p <$

0.001, Figure 3.8), but cheetahs' distances to the Reserve boundary were not affected by livestock abundance (-0.20 ± 0.15, $p = 0.17$).

Similar to cheetahs, the frequency of jackal sightings was significantly negatively correlated with the proportion of closed habitat (-3.01 ± 0.53, $p < 0.0001$, Figure 3.9) and positively correlated with livestock abundance (0.19 ± 0.10, $p = 0.06$). The distance from the Reserve boundary and livestock abundance had a significant interactive effect on jackal sightings (0.23 ± 0.04, $p < 0.0001$, Figure 3.10); jackal sightings were more frequent near the Reserve boundary when the abundance of livestock was relatively low, but during times of elevated livestock density, they appeared to move farther from the boundary. No statistically significant interactions were observed between the proportion of closed habitat and livestock abundance for any carnivore. Neither cheetahs' (-0.03 ± 0.09, $p = 0.74$) nor jackals' (0.03 ± 0.03, $p = 0.13$) space use were significantly correlated with lions' space use.

DISCUSSION

Our results suggest that lions and jackals avoided areas characterized by intense pastoral activity, because both species increased their distance to the Reserve boundary as a function of increasing livestock abundance. Livestock enter and exit the Reserve daily by crossing the river that separates the town of Talek from the Reserve. Cattle presence extends up to several kilometers into the Reserve, but the intensity of use by livestock is highest along the northern boundary and decreases with distance from this boundary (Boydston et al. 2003, Butt 2014). Cheetahs avoided the disturbed habitat along the Reserve boundary but did so independently of livestock abundance. None of our focal species exhibited attraction to areas heavily used by livestock; that is, none of them moved closer to the boundary in times of elevated livestock abundance.

Avoiding areas of intense use by herders and livestock should reduce human-caused mortality for large carnivores, but doing so could also keep them from accessing resources in those areas, such as water and prey (Boydston et al. 2003, Ogutu et al. 2014). Spotted hyenas are highly flexible in their behavior and have been shown to avoid open habitats such as grasslands in landscapes shared with livestock herds, instead using closed habitat to conceal themselves from herders (Kolowski & Holekamp 2009). We found the proportion of vegetative cover at a site to be the strongest predictor of use by lions, who selected sites containing closed habitat to those that were purely open habitat, such as grasslands. Cheetahs and jackals, on the other hand, were seen more often in open habitat. This could reflect differences in species' behavior, such as hunting strategy (ambush versus pursuit) and activity pattern, or species-specific detection probabilities in different habitats based on body size, coat pattern, or behavior. For example, cheetahs often perch on mounds in open plains to survey their surroundings, making them highly detectable when engaged in this behavior. Neither lions', cheetahs', nor jackals' habitat selection varied based on livestock abundance, suggesting that closed habitat did not facilitate fine-scale coexistence between pastoralists and native carnivores. In a study of the Greater Mara, including community land and conservancies, Klaassen & Broekhuis (2018) found that cheetahs outside the Reserve selected closed habitat, while we found that cheetahs inside the Reserve selected open habitat. One possible explanation for this difference is the variation in the perceived risks imposed by humans and lions across study sites, which could prompt cheetahs to adjust their patterns of habitat use accordingly.

Alternatively, the lack of evidence of habitat-mediated avoidance of humans (i.e., increased use of closed habitat with increasing livestock abundance) herein could also be an artefact of our methods of data collection. Previous studies of habitat selection in large carnivores in this ecosystem have derived location data from GPS collars (Klaassen & Broekhuis 2018) or have used VHF collars to help observers locate study animals (Kolowski & Holekamp 2009), whereas we used only opportunistic sightings. Therefore, we likely failed to detect carnivores if they were in dense vegetative cover, and we were unable to account for differential detection probabilities between habitat types. Still, even if our detection of carnivores in vegetation was low, patterns of their use of open habitats near versus far from the nearest available closed habitat as a function of livestock abundance is still valuable information.

We found interesting differences among species' behavioral responses to disturbance. Some previous work suggests that cheetahs avoid areas of human use more strongly than areas of lion use (Riggio et al. 2018, Klaassen & Broekhuis 2018), while other studies suggest the opposite (Elliot & Gopalaswamy 2017, Marker et al. 2003), potentially contingent on the intensity of human disturbance (Klaassen & Broekhuis 2018). In this study, cheetahs maintained the greatest distances to the Reserve boundary and exhibited similar space use patterns regardless of the intensity of pastoral activity within the Reserve, although we saw fewer cheetahs overall in times of high livestock abundance. Lions avoided the edge of the Reserve as well, but the strength of this avoidance varied with livestock density; of our three study species, lions displayed the strongest behavioral response to pastoralists and their livestock. This makes sense, given that lions are more frequently targeted for retaliatory, preemptive, and ritualistic killing by Maasai people than are cheetahs or jackals (Kissui 2008, Koziarski et al. 2016).

The most flexible space use was exhibited by jackals. Jackals were the least dominant and smallest of our three focal carnivore species and exhibited the most generalist diets, and they maintained the closest proximity to the edge of the Reserve. In fact, when livestock density was relatively low, jackals were seen more frequently near the boundary than deeper in the Reserve.

Since lions and cheetahs avoided the disturbed northern edge of the Reserve, this area may have provided jackals with refuge from intraguild competition and predation, a phenomenon sometimes referred to as the spatial "human shield" effect (Wilson et al. 2010, de Satgé et al. 2017, Karanth et al. 2017, Moll et al. 2018, Cervantes et al. 2023). With increasing pastoral activity, however, jackals' use of edge habitat declined, and when livestock grazing intensity was high, jackals – like lions and cheetahs – avoided the edge habitat. This suggests that jackals changed their strategy based on the greatest perceived risk. These jackals must navigate a complicated "landscape of fear," where they face risk of predation by native carnivores such as lions and cheetahs and by humans (Swanson et al. 2016, Gaynor et al. 2019, Kamler et al. 2020a).

One limitation of our study is that our observations are limited to daytime, specifically in the hours surrounding dawn and dusk. Therefore, we could not account for temporal partitioning of resources, only for long-term spatial partitioning. Specifically, we did not incorporate time of day as a predictor, and our observations completely excluded carnivores' nighttime movements. The presence of herders and livestock inside the Reserve varies with the time of day. Herders and livestock typically use the Reserve by day and return to their homes outside the Reserve at nighttime, where livestock are typically confined to enclosures called "bomas". However, herders sometimes adjusted their schedule to avoid detection by tourists and rangers, instead grazing livestock inside the Reserve only at nighttime. Lions and other carnivores may restrict their use of highly disturbed areas, areas near human settlements, and shared resources (such as watercourses) to nighttime in order to avoid conflict with humans (Valeix et al. 2012, Oriol-Cotterill et al. 2015a, Connolly et al. 2021). However, at coarse spatial scales, lions have been found to reduce their overall use of highly disturbed areas (Oriol-Cotterill et al. 2015b). Our results would best be interpreted as evidence that more strongly persecuted carnivores show stronger avoidance of areas near grazing activity during times of day when livestock are present than carnivores less prone to conflict with humans do.

The coarse temporal resolution of our data limited our ability to detect fine-scale temporal avoidance of dominant predators by subordinate predators. Swanson et al. (2016) found that coarse-scale space use by cheetahs and lions appeared to be positively correlated, because rather than proactively avoiding areas of high lion use altogether, cheetahs adjusted their hourly movements to reactively avoid lions in real time while still accessing quality habitat and important resources. However, even at the coarse temporal resolution of this study, it is curious that jackals did not avoid sites frequented by lions, given that Kamler et al. (2020b) found jackals to spatially partition space with lions even over long periods of time, avoiding parts of their home ranges used heavily by lions.

In addition to the coarse temporal resolution of our study and the restriction of data collections to two periods of daylight, our analytical approaches were restricted by the lack of data for spatial distributions of livestock and native ungulates. As a result of these three limitations, we were unable to address questions related to fine-scale temporal partitioning among lions, cheetahs, jackals, and livestock. However, the information gleaned from this study should still be relevant to managers of protected areas, because we examined the broadscale effects of Reserve management (strictness of livestock prohibition) on space use of large carnivores during the times of day when most tourists are seeking megafauna. We also exemplify how anthropogenic activity differentially affects carnivore species, for example, due to body size, hunting strategy, trophic level (apex predator vs. mesocarnivore), or cultural perceptions. The variation in anthropogenic effects on different sympatric large carnivore species is an important consideration for conservation planning in different systems and highlights a process by which human activity can induce behavioral changes in carnivores which, in turn, trigger trophic cascades (Smith et al. 2012, Suraci et al. 2019). While we do not provide guidelines for specific targets for maximum livestock density within a protected area, we provide empirical evidence that lions' space use is affected not just by the presence or absence of livestock, but by their density. Under sustainable densities of livestock and with appropriate husbandry methods, pastoralism may be compatible with ecological conservation, including that of large carnivores (Ogada et al. 2003, Niamir-Fuller et al. 2012).

The concept of the "landscape of fear" has great, but largely untapped, potential for protecting food security and biodiversity. Spatiotemporal partitioning serves as a mechanism for coexistence among sympatric carnivore species (Rostro-García et al. 2015, Swanson et al. 2016, Dröge et al. 2017, Klaassen & Broekhuis 2018, Searle et al. 2021), and large carnivores are known to exhibit similar patterns of spatial and temporal avoidance of humans and livestock (Oriol-Cotterill et al. 2015, Riggio et al. 2018, Klaassen & Broekhuis 2018, Miller & Schmitz 2019, Kautz et al. 2021). It stands to reason that this concept could inform the design and management of human infrastructure and activities, such as livestock grazing, to promote coexistence between humans and wildlife (Miller & Schmitz 2019). Schuette et al. (2013) found that spatial and temporal variation in Maasai herders' livestock grazing promoted coexistence between high densities of both livestock and lions on group ranches with minimal conflict by enabling lions to spatiotemporally avoid humans and livestock. Recognition is growing of the role of humans in modifying the spatial and temporal patterns of carnivore activity, including mediation of spatial and temporal partitioning among carnivores (Moll et al. 2018, Shores et al. 2019, Searle et al. 2021, Rodriguez Curras et al. 2022, Seveque et al. 2022), and how this can promote coexistence (Miller & Schmitz 2019). Incorporating this knowledge into Reserve management can improve innovation and efficacy of conservation and maintain the role of this land in the local community's culture, food security, and economy (Goldman 2011). We recommend that future studies continue to disentangle the effects of pastoralist activity on behavior and demography across carnivore species and begin testing specific grazing management strategies' potential for facilitating coexistence between humans and wildlife.

Finding ways in which livestock production and intact wildlife communities can share landscapes should be regarded as a top research priority. Livestock grazing occupies approximately 37% of the earth's ice-free land (Boronyak et al. 2020) and is likely to further expand (Forslund et al. 2023). Given future projections of land use change, protected areas alone will be insufficient to effectively conserve large carnivores (Di Minin et al. 2016), and even protected areas are often subject to intense anthropogenic pressure (Woodroffe & Ginsberg 1998). Thus, innovative strategies that allow carnivores to persist in landscapes shared with humans and livestock are urgently needed (Di Minin et al. 2016, Miller & Schmitz 2019, Boronyak et al. 2020, 2022).

TABLES

Table 3.1

We investigated patterns of distance-sensitive avoidance and habitat-mediated avoidance of pastoralists and their livestock by large carnivores, as well as how mechanisms of attraction or avoidance varied among sympatric carnivore species. The table below summarizes our study questions and the associated hypotheses and predictions proposed.

Study Question	Hypothesis	Prediction
How did pastoral activity affect carnivores' proximity to livestock herds?	Carnivores avoid herders and livestock (distance-sensitive avoidance).	Distance to the Reserve boundary and livestock abundance have a significant positive interactive effect on carnivore sighting frequency.
	Carnivores are attracted to livestock.	Distance to the Reserve boundary and livestock abundance have a significant negative interactive effect on carnivore sighting frequency.
How did pastoral activity affect carnivores' habitat selection?	Carnivores increase their use of closed habitat in response to increased disturbance by herders and livestock.	Proportion of closed habitat at a given site and livestock abundance have a significant positive interactive effect on carnivore sighting frequency.
How did pastoral activity affect spatial partitioning within the carnivore guild?	All three study species respond similarly to the presence and density of herders and livestock.	Similar interactive effects (distance to Reserve boundary x livestock abundance, proportion of closed habitat x livestock abundance) are observed for all three study species.
	Subordinate predators' space use is affected more strongly by dominant carnivores' presence than by the presence of herders and livestock.	Interactive effects of opposite directions will be observed between carnivore species.

FIGURES

Figure 3.1

The inset map shows the extent of the entire Reserve, represented by a gray polygon, and our study area, indicated in red. In the main image, our study area is shaded gray, and is bound on its northernmost edge by the Reserve boundary, which is the Talek River. To exemplify how we accounted for observer effort, all tracks driven within a single month-year during our study period (November 2012) are represented by black lines. The total length of tracks driven per each month-year were for each cell within a 400 x 400 m resolution fishnet grid, shown in red.

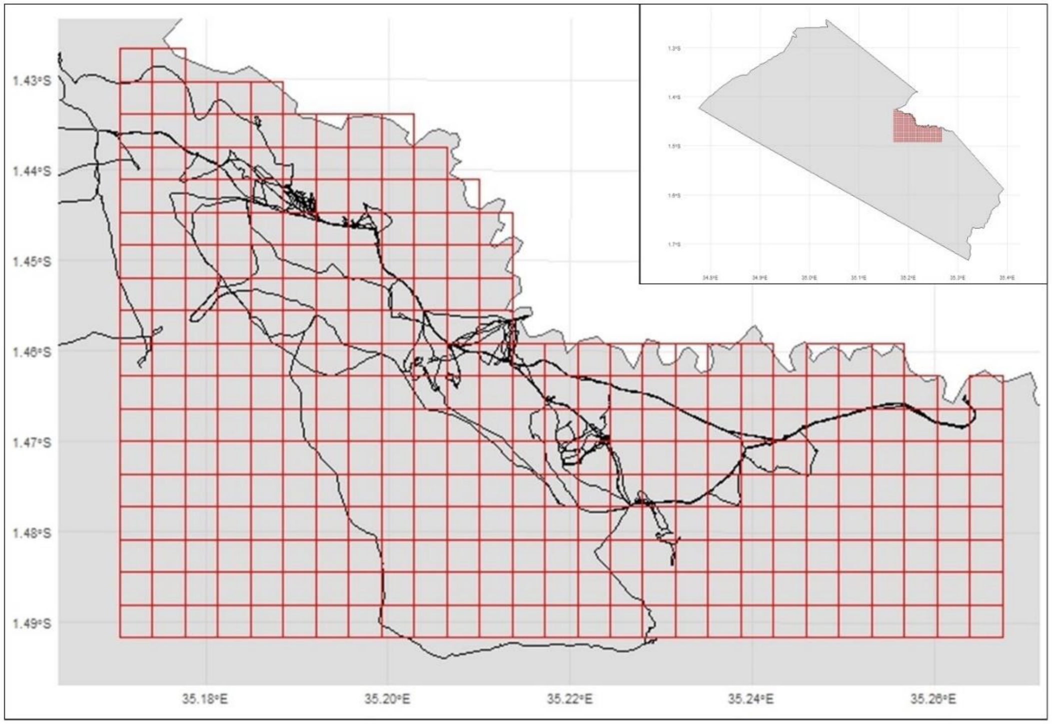


Figure 3.2

Bars and whiskers show the means and 95% confidence intervals, respectively, of total monthly precipitation from 2013-2019.

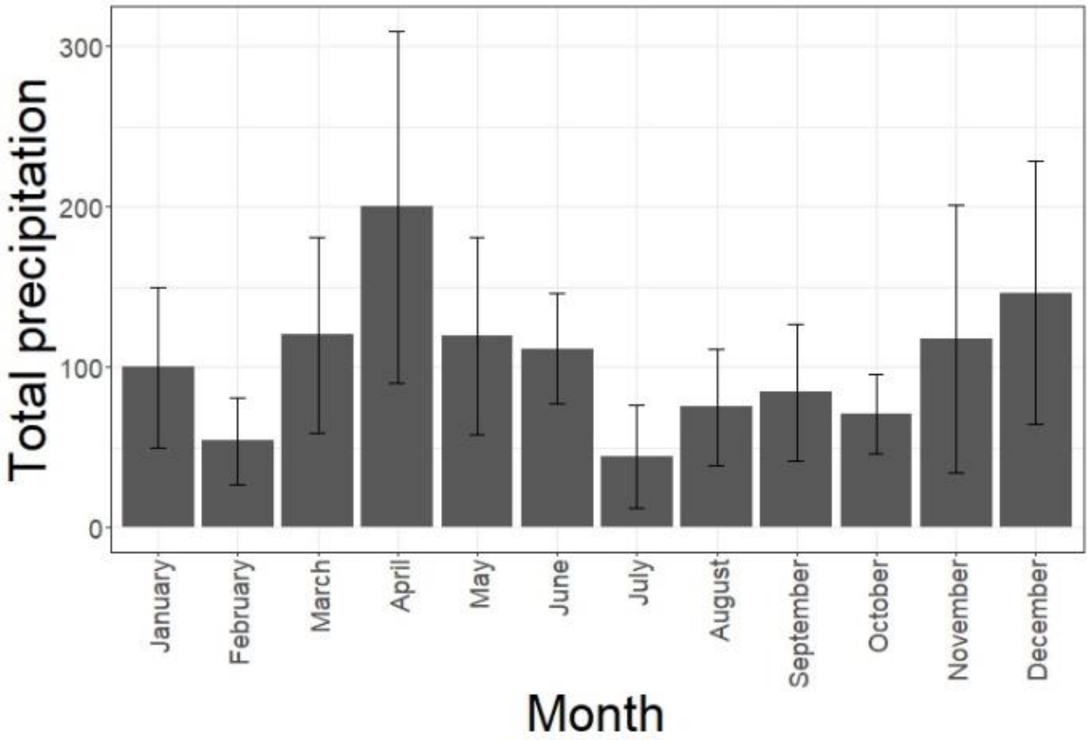


Figure 3.3

Bars and whiskers show the means and 95% confidence intervals, respectively, of the total number of native ungulates counted on four-kilometer prey transects from 2013-2019.

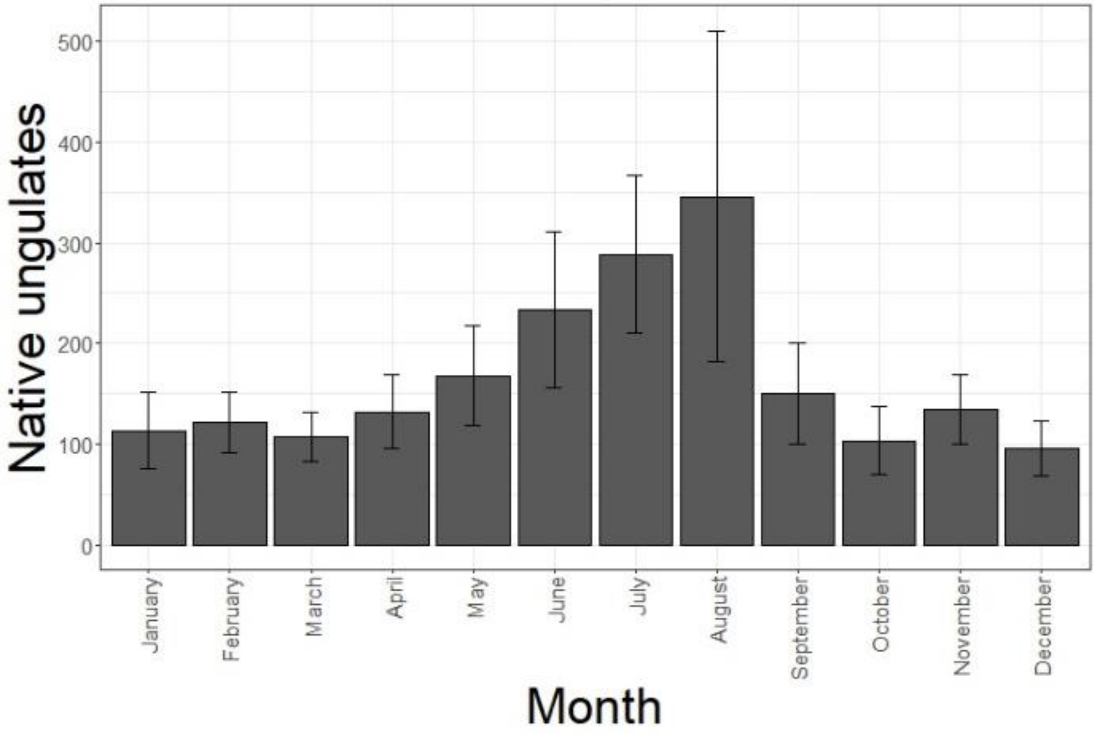


Figure 3.4

Bars represent the mean abundances of cattle (purple), shoats (green), and cattle and shoats combined (gold) inside our study area each month, and whiskers represent the 95% confidence intervals. Abundances varied widely, but the total livestock abundance started increasing in December, reaching its peak in March. Cattle typically outnumbered shoats.

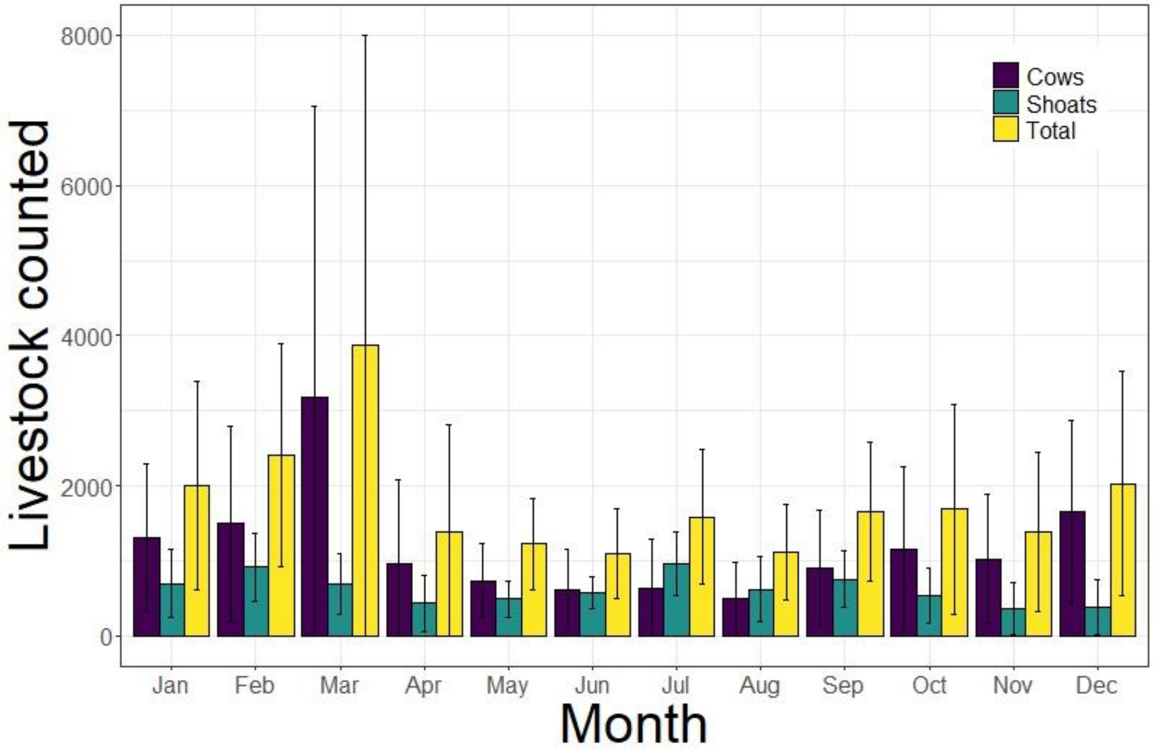


Figure 3.5

Bars represent the mean abundances of cattle (purple), shoats (green), and cattle and shoats combined (gold) inside our study area each year, and whiskers represent the 95% confidence intervals.

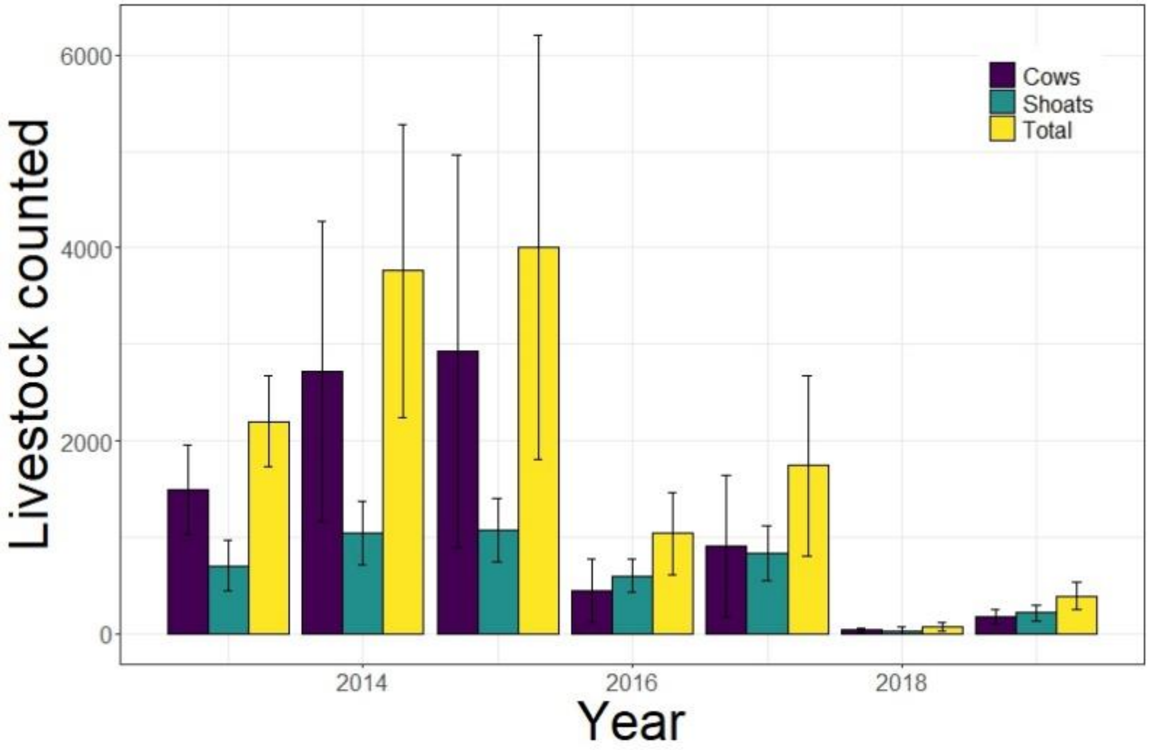


Figure 3.6

Points and whiskers represent the slope (*β*) estimates and 95% confidence intervals, respectively, for main effects on space use by lions at the intermediate (400 x 400 m) resolution. Expected counts of lion observations were significantly positively predicted by the distance to the Reserve boundary (*β* = 0.60, 95% CIs = 0.29 to 0.90, $p < 0.001$) and the proportion of vegetative cover (*β* = 5.49, 95% CIs = 2.39 to 7.59, $p < 0.001$).

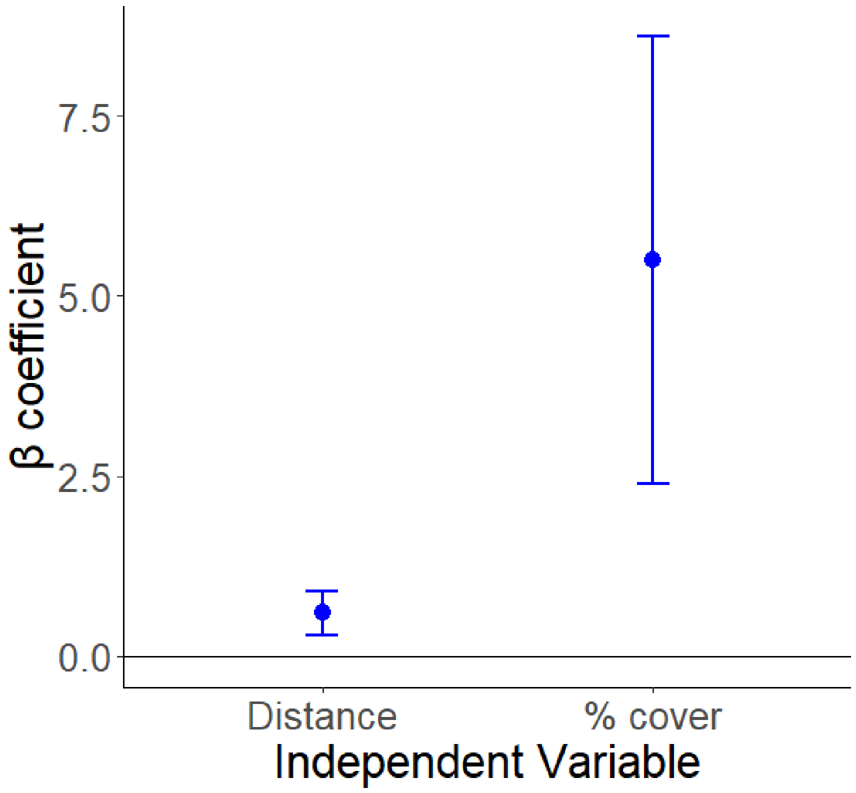


Figure 3.7

Here, the site-specific predicted counts of lions as a function of standardized distance from the Reserve boundary are shown at the intermediate spatial resolution for 100, 1000, and 4000 livestock; lines and shaded regions indicate predictions ± std. err., respectively. Lions were less commonly seen across the study area with increasing livestock abundance (β ± std. err = -0.74 ± 0.35, $p < 0.05$; main effect). Site-specific space use by lions increased with distance to the Reserve boundary (0.60 ± 0.16, $p < 0.001$; main effect), and the positive effect of distance to boundary was stronger with increasing livestock abundance (0.62 ± 0.21, $p < 0.01$; interaction).

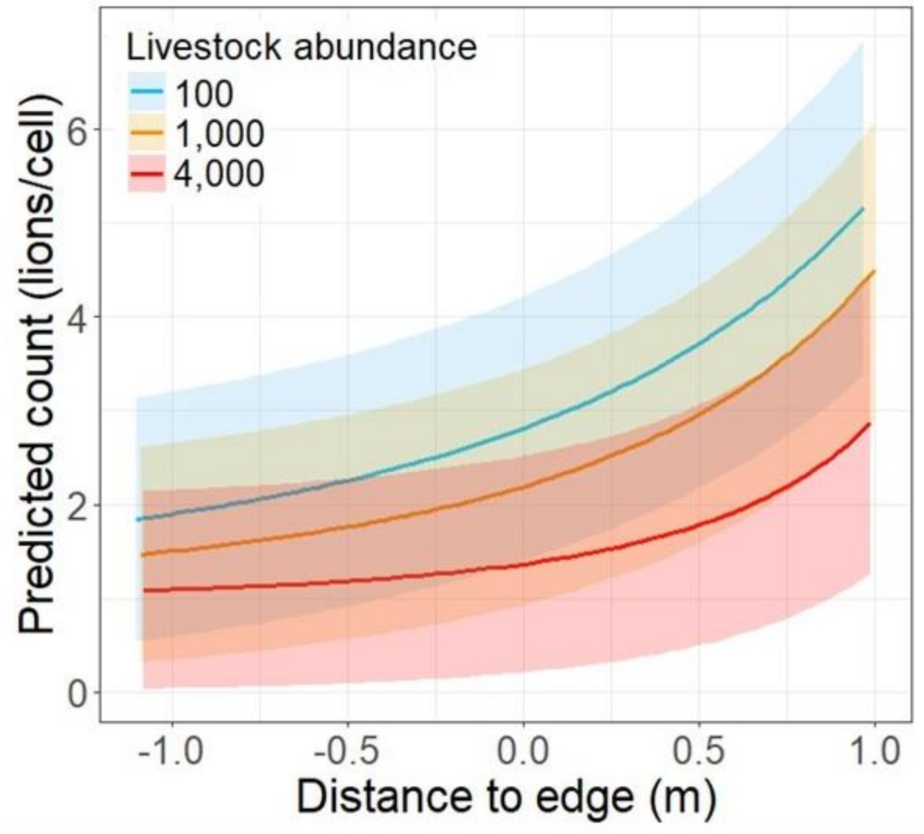


Figure 3.8

Points and whiskers represent the slope (*β*) estimates and 95% confidence intervals, respectively, for main effects on site-specific space use by cheetahs at the intermediate (400 x 400 m) resolution. Expected counts were significantly positively predicted by the distance to the Reserve boundary (*β* = 0.60, 95% CIs = 0.28 to 0.92, *p* < 0.001). Expected counts decreased with increasing proportion of vegetative cover, and this effect was almost statistically significant (*β* = -4.44, 95% CIs = -8.97 to 0.09, *p* = 0.055). Site-specific use by lions had a negligible and nonsignificant effect on space use by cheetahs (*β* = -0.03, 95% CIs = -0.21 to 0.15, *p* = 0.74). Significant positive effects are shown in blue, and nonsignificant negative effects are shown in orange.

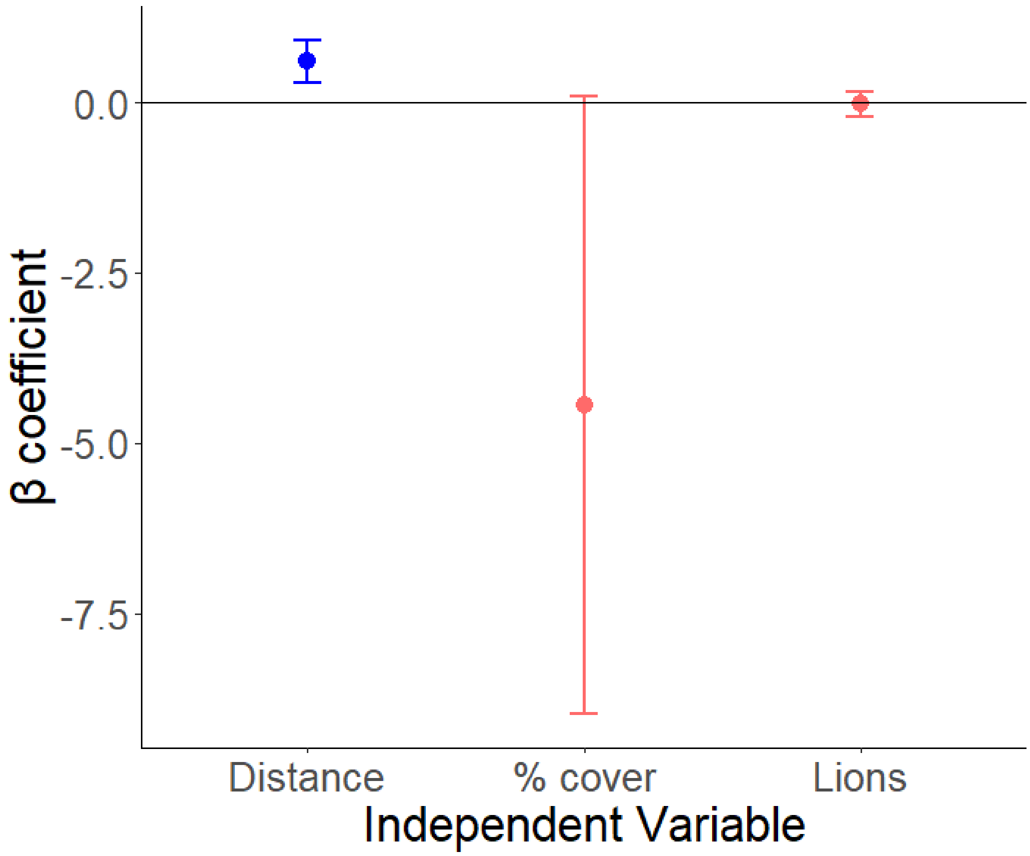


Figure 3.9

Points and whiskers represent the slope (*β*) estimates and 95% confidence intervals, respectively, for main effects on site-specific space use by jackals at the intermediate (400 x 400 m) resolution. Expected counts were strongly negatively correlated with the proportion of vegetative cover (*β* = -3.01, 95% CIs = -4.05 to -1.96, $p < 0.0001$). Microhabitat use between jackals and lions showed a small but statistically significant positive correlation (*β* = 0.04, 95% CIs = -0.01 to 0.09, $p = 0.13$). This correlation was not evident at coarser spatial resolutions. The distance to the Reserve boundary alone did not affect jackals' space use (*β* =-0.05, 0. 95% CIs = -0.14 to 0.04, $p = 0.26$). Significant positive effects are shown in blue, nonsignificant positive effects are shown in turquoise, and significant negative effects are shown in red.

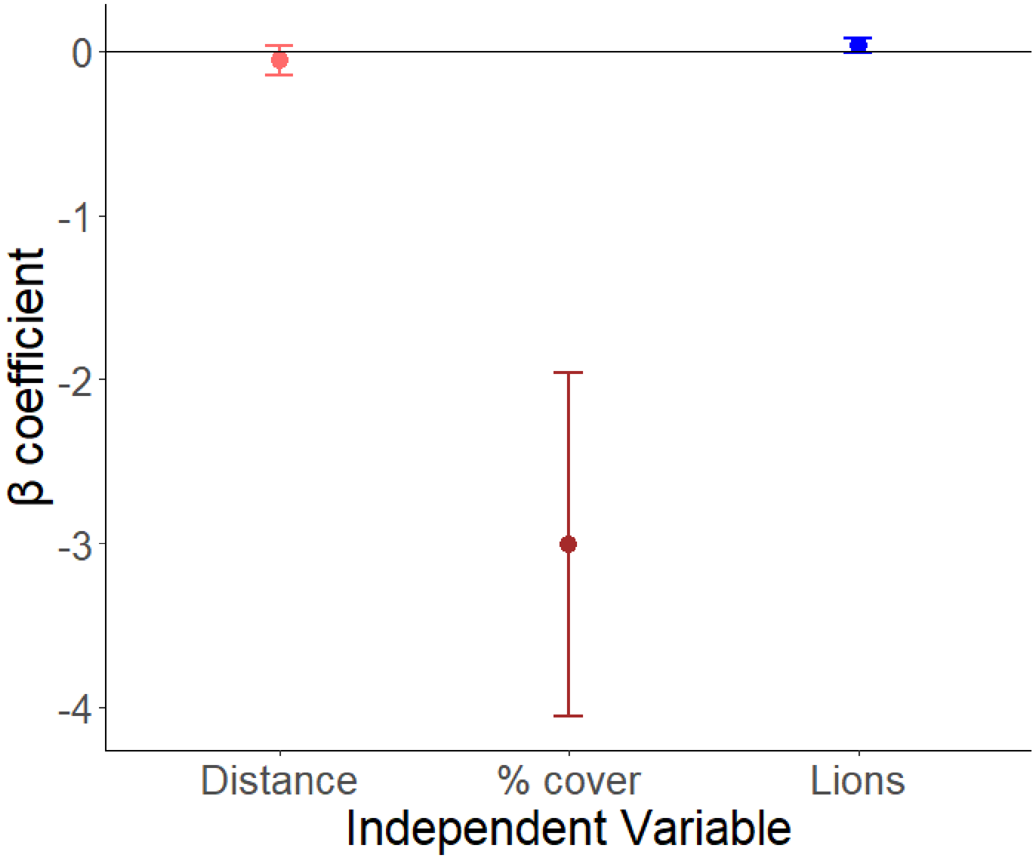
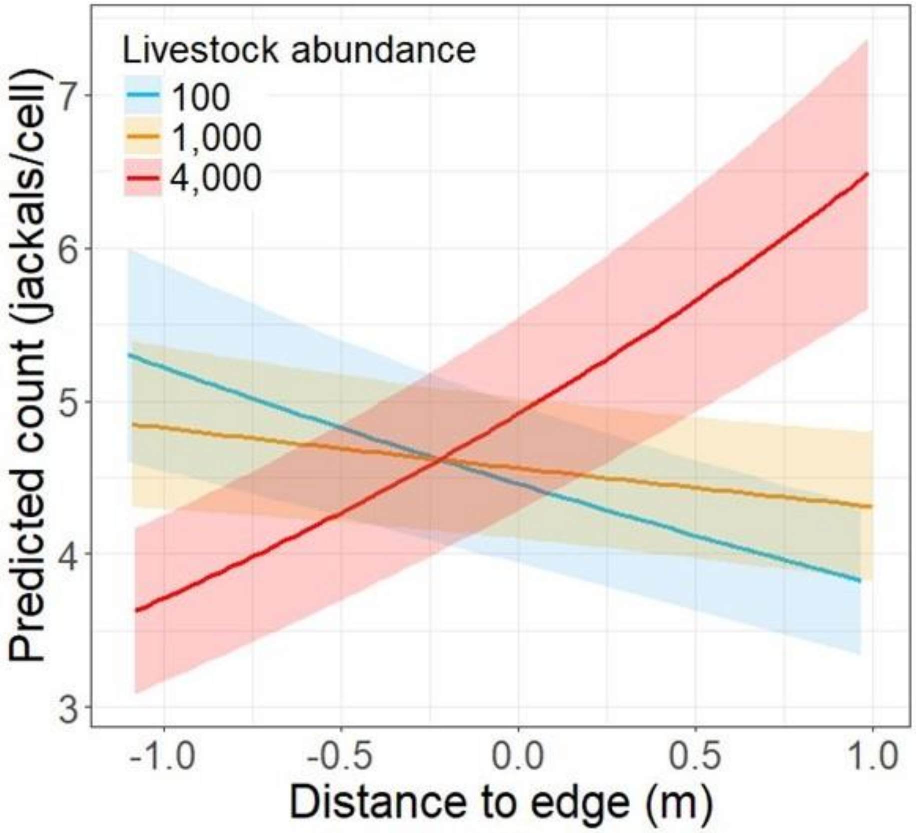


Figure 3.10

Here, the site-specific predicted counts of jackals as a function of standardized distance from the Reserve boundary are shown at the intermediate spatial resolution for 100, 1000, and 4000 livestock; lines and shaded regions indicate predictions + std. err., respectively. We found a positive trend between the frequency of jackal sightings and livestock abundance (β + std. err = 0.19 + 0.10, p = 0.06; main effect). The distance to the Reserve boundary, by itself, did not significantly predict jackal sighting frequency (-0.05 + 0.-5, p = 0.26; main effect), but we found a significant interactive effect of livestock abundance and distance to Reserve boundary on jackal sighting frequency (0.23 + 0.04, p < 0.0001; interaction). At low to moderate livestock abundances, jackal sighting frequency was highest near the Reserve boundary. When livestock abundance was high, jackal sightings became more frequent with increasing distance to the boundary.



CHAPTER 4:

THE VALUE OF INDIVIDUAL IDENTIFICATION IN STUDIES OF FREE-LIVING HYENAS AND AARDWOLVES

ABSTRACT

From population estimates to social evolution, much of our understanding of the family Hyaenidae is drawn from studies of known individuals. The extant species in this family (spotted hyenas, *Crocuta crocuta*, brown hyenas, *Parahyaena brunnea*, striped hyenas, *Hyaena hyaena*, and aardwolves, *Proteles cristata*) are behaviorally diverse, presenting an equally diverse set of logistical constraints on capturing and marking individuals. All these species are individually identifiable by their coat patterns, providing a useful alternative to man-made markings. Many studies have demonstrated the utility of this method in answering a wide range of research questions across all four species, with some employing a creative fusion of techniques. Despite its pervasiveness in basic research on hyenas and aardwolves, individual identification has rarely been applied to the conservation and management of these species. We argue that individual identification using naturally occurring markings in applied research could prove immensely helpful, as this could further improve accuracy of density estimates, reveal characteristics of suitable habitat, identify threats to population persistence, and help to identify individual problem animals.

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INTRODUCTION

Our understanding of the biology of many mammals, including mammalian carnivores, has been greatly enhanced by studies of individually recognizable animals (Clutton-Brock & Sheldon 2010, Schneider et al. 2019, Karczmarski et al. 2022a, 2022b). Such studies have shed light on demography, natural selection, life histories, ontogeny, social behavior, and intrapopulation variation in diverse species and populations (Clutton-Brock & Sheldon 2010). In free-living populations, however, capturing and marking individuals (Mills 1982a, 1983a, 1983b) may be impractical due to limited funds, difficulty obtaining permits, rarity or elusiveness of subjects, or – in some group-living species – a large number of subjects, making it impractical to capture every individual in the study population. Individual identification using naturally-occurring markings is a practical, cheap, and noninvasive alternative to capturing and marking wild animals (Powell & Proulx 2003, Mendoza et al. 2011, Kelly et al. 2012, Schneider et al. 2019). This method has been applied to various mammalian carnivores with unique pelage patterns (Karanth & Nichols 1998, Heilbrun et al. 2003, Harihar et al. 2010). Even in more subtly marked species, individuals can be consistently differentiated using whisker patterns (Anderson et al. 2007, Osterrieder et al. 2015, Elliot & Gopalaswamy 2017), coloration, facial markings, leg and tail markings, body and tail structure or carriage, kinks in tails, ear nicks, or scars (Trolle et al. 2006, Kelly et al. 2008, Sarmento et al. 2009, Zheng et al. 2016). Natural markings are used to identify individual animals both in direct observations (Smith et al. 2017) and during use of camera traps (Dheer et al. 2022).

Studies of individually known members of the family Hyaenidae have proven particularly fruitful. This family contains only four extant species, but these species exhibit impressive diversity in morphology, diet, and social organization. The three bone-cracking hyena species include spotted (*Crocuta crocuta*), brown (*Parahyaena brunnea*), and striped (*Hyaena hyaena*) hyenas. Although spotted hyenas kill most of their own prey, the other two bone-cracking forms live mainly on carrion. By contrast, aardwolves (*Proteles cristata*) feed almost exclusively on termites. These species span a wide spectrum of social behavior, from aardwolves, which are solitary except when breeding, to spotted hyenas, which sometimes live in the largest groups of any terrestrial carnivore (Green et al. 2018). The diversity within this family makes these species excellent models for basic research. Furthermore, human-hyena conflict and the Near Threatened status of brown and striped hyenas (AbiSaid & Dloniak 2015, Wiesel 2015) suggest that further study of these animals should facilitate their conservation and management.

In this review, we briefly describe the morphology and ecology of each extant species in the family Hyaenidae and describe how best to distinguish individuals based on their unique markings. We then highlight studies of demographic and socioecological processes that illustrate the utility of individual identification in studies of free-living hyaenids. Finally, we discuss previous applied work using individual identification, and identify important gaps in our knowledge of hyaenids that could be filled using the identification methods we describe.

The four extant hyaenid species

Spotted hyenas are large, gregarious carnivores that occur throughout much of sub-Saharan Africa. Adults typically weigh roughly 55.00 kg and stand 0.77-0.80 m tall at the shoulder, with females being about 10% larger than males (Swanson et al. 2013), making spotted hyenas the largest of the extant hyaenids. Their fur ranges in color from sandy to grey or brown, with dark spots on their flanks, backs, rumps, and legs (Holekamp & Kolowski 2009). The spotted hyena is the only extant hyaenid whose post-cranial anatomy is adapted for cursorial hunting of medium- and large-sized herbivores, and 65-95% of their diet consists of prey they kill themselves (Holekamp & Dloniak 2010). Spotted hyenas exhibit social behavior convergent with that of cercopithecine primates. They live in stable, fission-fusion social groups, called “clans,” that may contain up to 126 individuals (Green et al. 2018). Each clan is structured by a linear dominance hierarchy in which adult females outrank most breeding males. Although they are experiencing global decline, spotted hyenas are still abundant throughout sub-Saharan Africa, and are listed as a species of Least Concern by the International Union for Conservation of Nature (IUCN; Bohm and Höner 2015).

Brown hyenas occur in southern Africa, where they are widespread throughout Botswana (Winterbach et al. 2017) and most of Namibia (Wiesel 2015). They also occur in Angola, Zimbabwe, and South Africa. Body size varies regionally, with adults weighing 28.00-47.50 kg, and typically standing around 0.74 (females) or 0.79 (males) m tall at the shoulder (Holekamp & Kolowski 2009). Their long, shaggy fur is dark or reddish brown on their torsos and has a lighter tawny color on their necks and shoulders. The face is covered with short, dark hair, and their front and hind legs are striped. They are opportunistic foragers, feeding mainly on vertebrate remains. Hunting plays a minor role in this species, although brown hyenas living along the southern Namib Desert coast regularly kill Cape fur seal (*Arctocephalus pusillus pusillus*) pups at mainland seal colonies (Wiesel 2010). Brown hyenas live in small clans of four to 14 individuals, within which females sometimes breed cooperatively (Mills 1982b, 1990). Males either remain in their natal clan, disperse to a new clan to breed, or become nomadic breeders. The IUCN lists this species as Near Threatened, with a population estimate of fewer than 10,000 mature individuals (Wiesel 2015).

Striped hyenas have the largest geographic range of the extant hyaenids, stretching from the northwestern coast of Africa and as far south as Tanzania, through the Middle East and the southern Caucasus, and eastward through much of India (AbiSaid & Dloniak 2015) and into Nepal (Bhandari et al. 2020). They are smaller than spotted or brown hyenas, typically weighing 26.00-41.00 kg and standing 0.66-0.75 m tall at the shoulder. Striped hyenas have a somewhat shaggy appearance, a bushy tail, and the most prominent mane of any hyaenid. They have black muzzles, black throat patches, and black or brown stripes on lighter-colored fur (Holekamp & Kolowski 2009). These hyenas are omnivorous scavengers that hunt infrequently and opportunistically (Kruuk 1976, Holekamp & Kolowski 2009). Despite their expansive range and ecological importance (Beasley et al. 2015), they remain poorly understood. This void in information is likely due to their low density, nocturnality, elusiveness, the rough terrain they sometimes inhabit, and confusion with spotted hyenas where the two species co-occur (Kruuk 1976, Holekamp & Kolowski 2009). Traditionally, striped hyenas have been considered solitary (Kruuk 1976), but recent research suggests that this is not the case for all populations (Wagner et al. 2008, Califf et al. 2020, Tichon et al. 2020). The striped hyena has been extirpated from many parts of its range, and populations continue to decline globally. Conservation of this Near Threatened species requires further research on its behavior and demography (Mills & Hofer 1998, Holekamp & Kolowski 2009, AbiSaid & Dloniak 2015).

Aardwolves occur in East and southern Africa (Green 2015). As the smallest member of the hyena family, they typically weigh 8.00-12.00 kg and stand 0.45-0.50 m tall at the shoulder (Holekamp and Kolowski 2009). Aardwolves feed predominantly on termites (*Trinervitermes spp.;* Kruuk & Sands 1972, Koehler & Richardson 1990, Anderson 2013, Green 2015). They are primarily nocturnal and forage alone (Smithers 1983, Koehler and Richardson 1990, Anderson 2013). During the breeding season, mated pairs of aardwolves occupy a territory with their youngest offspring (Koehler and Richardson 1990, Richardson 1991). The conservation status of aardwolves is listed as Least Concern, and their global population is considered stable (Green 2015).

Individual identification by naturally-occurring markings

All four hyena species have unique coat patterns that are consistent throughout the animals' lives. Individuals can be distinguished using these markings and any other unique characteristics, such as scars or ear damage. To avoid misidentification, reference photographs must be maintained for each study population, preferably including high-quality reference photos of the left and right sides of each animal, as the markings on the two sides differ. Such images can be obtained easily by taking video footage of both sides of an individual animal as it moves around, freezing the frames in which left- and right-side markings are clearest, and printing those images. If photographs of each individual's left and right side cannot be matched for any reason, two separate sets of records should be kept, one for the right-side images and one for left-side images (Karanth 1995), and they should be analyzed separately (Gupta et al. 2009, Harihar et al. 2010, Kent & Hill 2013, Dheer et al. 2022). Identification relies on distinctive patterning of the coat in all four species, so images need not be in color; in fact, converting photographs to black and white and increasing the contrast may be helpful for maximizing clarity of coat patterns. Images may be annotated with useful, unique markings. In any case, these databases require upkeep as new individuals are born or immigrate and existing hyenas develop new scars or injuries, emigrate, or die. Digital reference photographs of known individuals may be most useful for identifying animals in camera trap images, as they allow the observer to zoom in on individual body parts (Henschel & Ray 2003). Although future technological advances may lead to digital devices that are practical for field identification, in general, hard copies of reference photos are currently necessary for identification during direct observations. Hard copies of reference photos also serve as invaluable backup records. If time allows, photographs can be taken of individuals in the field and immediately compared to the reference photos to confirm identities. It is important that the observer uses spots or stripes from multiple body parts whenever possible to confirm an identity. Before they can identify individuals without their work being checked by an expert, observers need a substantial period of training. An expert should observe their work and decide when new observers are ready to work independently. Ideally, two or more independent observers will confirm each identity.

Spotted hyenas

Long-term (1979 to present, Holekamp & Strauss 2020, 1987 to present, Hofer & East 1993) and shorter-term (Henschel & Skinner 1990) studies of spotted hyenas demand that observers be able to recognize each hyena individually based on its unique spot patterns, ear damage, and other permanent markings (e.g., missing tail, significant scars). Fortunately, except after mud-bathing, individuals are recognizable, as they have unique, permanent spot patterns that vary among individuals (Figure 4.1). The Mara Hyena Project (Kenya) maintains a photo album for each of its study clans showing left- and right-side spot patterns of each clan member (Figure 4.2a). Photo albums for all nearby study clans are also carried in each research vehicle during data collection. Position and shape of ear damage (e.g., cut, notch, missing ear; Figure 4.2b), when present, also aids in individual identification, but examining spot patterns in reference photos is critical to confirm identities, even for highly experienced observers. Different age-sex classes (i.e., cub, subadult, adult female, adult male) have different body-shape profiles (Johnson-Ulrich et al. 2018), so organizing photos by age-sex class reduces the number of spot patterns one must check for confirmation. Further dividing adult hyenas into residents and “aliens” can further facilitate the process of individual identification. Hyenas that are seen passing through the territory of a study hyena clan that are not members of that particular clan are considered “aliens”; these are often dispersing males. Thus, we recommend organizing each photo album into five sections: cubs, subadults, resident adult females, resident adult males, and “aliens”.

Spotted hyena cubs are seldom seen aboveground before they are a few weeks old. They are born with solid dark brown or black natal coats, and, upon first seeing them, their age can be estimated to within seven days based on their pelage, size, and other features (Pournelle 1965, Holekamp et al. 1996). Although cubs are often difficult to tell apart before replacement of the natal coat, this can sometimes be done based on slight differences in fur color, size differences, patterns of abrasion on the skin covering the carpal bones, small nicks in the ears (often inflicted during the early fighting between litter-mates; Frank et al. 1991; Figure 4.3), and differential patterns of scarring on cubs’ backs, necks, and shoulders. Although female spotted hyenas have male-like genitalia, one can determine the sex of each cub older than a few weeks by using the dimorphic morphology of the glans of the erect phallus (Frank et al. 1990, Cunha et al. 2003, McCormick et al. 2021, Dheer et al. 2022). Cubs change somewhat in appearance as they grow, mainly due to having fur of variable length and texture between consecutive molts, but, once the spot pattern appears, it never changes. The spots typically begin to fade by the time a hyena reaches its mid-teens and continue fading as the hyena ages. The oldest hyenas recorded by the Mara Hyena Project were 26 years old at the time of their deaths.

There is a lack of consistent criteria to define age-sex classes of spotted hyenas, and definitions of the age classes used are project-specific (e.g., Trinkel et al. 2004, Höner et al. 2005, Belton et al. 2018). For example, Holekamp et al. (2012) consider hyenas to be subadults once they are no longer dependent on the communal den, which typically happens at nine to 12 months of age, whereas Kruuk (1972) defines subadults based on a specific range of tooth-wear values. Similarly, females may be considered adults when they are first known to conceive litters, when their teeth are worn down to a certain degree, or when they reach a specific age.

Brown hyenas

Before the advances of digital photography and camera trap technologies, triangular ear notches were cut into brown hyenas' ears for quick individual identification (Mills 1982a, 1983a, 1983b). However, because man-made and natural ear notches may change over time (Figure 4.4), they are not a reliable stand-alone method of identification. Instead, the Brown Hyena Research Project (Namibia) distinguishes individuals by the unique stripe patterns on their fore- and hindlegs. Brown hyena cubs have no solid natal coat, and their leg stripes are faintly visible from birth, and become clearer as the hyenas grow. These stripes are permanent over the course of a hyena's lifetime (Figure 4.5), but their appearance is greatly influenced by the viewing angle (Figure 4.6). The stripes are often indistinct, due to the small and round surface area of the legs, and the sometimes-changing directional position of the hair. Therefore, the combined use of stripes on the anterior, lateral, and medial surfaces of the forelegs, stripes on the lateral surfaces of the hindlegs, and any ear notches result in the highest likelihood of correct identification. Photographs of the anterior surfaces of the forelegs as well as the left and right sides of the body should be maintained for identification purposes. Unlike spotted hyenas, female brown hyenas do not have masculinized genitalia, but external morphology is otherwise similar between sexes and they are generally considered to be sexually monomorphic (Mills 1982a, Butler-Valverde et al. 2015, Dheer et al. 2022). As a result, it is generally not possible to distinguish between males and females in the field without capture.

Striped hyenas

Striped hyenas have vertical stripes on their flanks, and diagonal and horizontal stripes on all four limbs (Holekamp & Kolowski 2009). They have no natal coat and, instead, are born sporting clear, conspicuous stripes (Rieger 1979, Bothma & Walker 1999). The position and shape of these stripes is consistent throughout a hyena's lifetime, although they may become distorted with seasonal variation in coat length or fade slightly with age (Rieger 1979, Jhala 2013). Striped hyenas can be individually identified by the patterns of stripes and dots on their shoulders, flanks, hips, forelimbs, and hindlimbs, as well as by any other conspicuous features (e.g., ear notches, scars; Figure 4.7). Stripes on the hind- (hip and upper hindleg) and forequarters (shoulder and foreleg) are the most useful, as they are prominent and vary between individuals (Singh 2008, Harihar et al. 2010), while stripes on the flank may be distorted by shaggy fur. One should use stripe patterns from multiple body parts to confirm individual identification (Gupta et al. 2009). Determination of sex is difficult without capture (Dheer et al. 2022) but may be possible for females that have dependent cubs, for example, if they are visibly lactating or being followed by their cubs (Alam 2011, Tichon et al. 2020).

Aardwolves

The coats of aardwolves are yellowish in color and the face and throat are grayer than the rest of the body. They have three or more vertical black stripes on each flank, and one or two diagonal stripes across their fore- and hindquarters. Irregular horizontal stripes run across the legs, and are darkest near their feet. Stripes and spots are sometimes present on the neck (Smithers 1983, Koehler & Richardson 1990). Individuals can be distinguished using their stripe and spot patterns (Richardson 1991, Silwa 1996, O'Brien & Kinnaird 2011, Rich et al. 2019; Figure 4.8). Coat patterns can also be paired with natural scars and ear nicks, if present

(Richardson 1991, Silwa 1996). Natural features have also been supplemented with reflective collars and man-made ear notches to aid in recognition (Richardson 1987a, 1987b, 1990, 1991, Silwa 1996). Visual determination of sex is unlikely to be feasible without capture (Dheer et al. 2022).

PAST AND PRESENT USE IN BASIC RESEARCH

Our knowledge of the ecology of the four hyaenid species has been acquired, in large part, from studies taking advantage of natural markings. Here we describe findings from selected studies that have used this method to address a wide array of research questions about hyaenids. This body of literature is vast, particularly for spotted hyenas, and this is by no means intended to represent a comprehensive overview of the literature. Rather, the studies highlighted here are meant to serve as examples of the diversity of past and present applications of this method and to demonstrate its value in basic research.

Individual recognition of wild hyaenids has greatly improved the accuracy with which we can assess their demography. Most large carnivores, including hyaenids, are rare, elusive, primarily nocturnal, or maintain large home ranges, making them difficult to detect (Cozzi et al. 2013, Chutipong et al. 2014, Green et al. 2020). Low detection probability renders common methods for estimating density of large terrestrial mammals, such as aerial transects and line surveys, inappropriate for these carnivores (Cozzi et al. 2013). Instead, density estimates for some large carnivores were historically based on call-in (also known as call-up) station surveys and sign surveys (most commonly track counts), which are demonstrably unreliable (Karanth & Nichols 1998, Kelly et al. 2012, Vissia et al. 2021). Photographic capture-recapture analyses of individually identifiable animals in camera trap images represents a substantial methodological advance over call-in station and sign surveys. Since its first application to estimating tiger

(*Panthera tigris*) abundance and density in India (Karanth 1995, Karanth and Nichols 1998), photographic capture-recapture has emerged as a powerful method for quantifying population characteristics of elusive carnivores (Treves et al. 2010, Kelly et al. 2012, Johansson et al. 2020). Camera traps were deployed in the field by 2007 for brown hyenas (Thorn et al. 2009), 2007-2008 for striped hyenas (Gupta et al. 2009, Harihar et al. 2010, Singh et al. 2010, Athreya et al. 2013), and 2008 for aardwolves (O'Brien & Kinnaird 2011). Photographic capture-recapture has been used to estimate the density of spotted hyenas in many countries throughout their geographic range, such as Congo (Henschel et al. 2014, Bohm 2015), Uganda (Braczkowski et al. 2022), Kenya (O'Brien & Kinnaird 2011), Botswana (Rich et al. 2019, Vitale et al. 2020), Namibia (Stratford et al. 2020), and South Africa (de Blocq 2014). In rare cases in which all study animals were known from extensive long-term direct observations, researchers derived precise counts of spotted hyenas within their study area (rather than using capture-recapture methods to estimate abundance; Watts & Holekamp 2009, Green et al. 2018), but extensive direct observations yield a better return-on-investment for behavioral studies than for population estimation (de Blocq 2014). In addition to population size, studies of known individuals have yielded estimates of other demographic parameters, such as population growth rate (Benhaiem et al. 2018, Green et al. 2018, Mandal 2018), mortality rate (White 2005, Watts & Holekamp 2009, Höner et al. 2012, Mandal 2018), birth rate (Holekamp & Smale 1995, Watts & Holekamp 2009), and sex ratio (Holekamp & Smale 1995).

Incorporation of environmental data into models of spatial or temporal variation in demographic parameters can reveal processes underlying population ecology. For example, the past decade has revealed several ecological correlates of striped hyena population characteristics. Singh et al. (2010, 2014) found that, unlike in other parts of their geographic range, striped hyenas in Rajasthan, India occurred at higher densities closer to human settlements than farther away. They posited that this high density was supported by the availability of unexploited livestock carcasses near settlements. They also found rugged terrain and forest cover to be important components of suitable habitats for striped hyenas in India, likely because they provide undisturbed den sites and daytime refugia where hyenas can rest undetected by humans and domestic dogs (Singh et al. 2010, 2014). In another Indian population of striped hyenas, vehicular traffic regulation had tremendous effects on rates of survival and population growth (Mandal 2018).

Studies of spatial and temporal variation in population size have aimed to illuminate ecological drivers of demography in spotted hyenas as well. In the Maasai Mara National Reserve, Kenya, the Talek hyena clan, which became known as the Talek West clan after a permanent clan fission event in 2000, has been studied from 1988 to present. Observers know each hyena by its unique natural markings and opportunistically collect biological samples (for genetic, dietary, hormonal, and other analyses) and fit hyenas with collars (VHF and/or GPS). The size of the Talek clan remained remarkably stable between 1989 and 1995 (Figure 4.9; Green et al. 2018), given that outbreaks of rabies (1989-1991) and canine distemper (1994-1995) decimated sympatric populations of African wild dogs (*Lycaon pictus*, Macdonald 1992, Alexander & Appel 1994, Kat et al. 1995) and lions (*Panthera leo*, Roelke-Parker et al. 1996, Kock et al. 1998), respectively. The slight reduction in hyena clan size in 1989 (Figure 4.9, Green et al. 2018) was due to emigration rather than increased mortality. This is consistent with previous findings documenting strong resistance of spotted hyenas to diseases that substantially increase mortality among sympatric carnivore species (Alexander et al. 1995, East et al. 2001, 2004, Watts & Holekamp 2009). However, disease-induced mortality has certainly been recorded for spotted hyenas (Roelke-Parker et al. 1996), including a *Streptococcus* outbreak that correlated with a 78% increase in mortality and slight population decline for two years in a spotted hyena population in the Ngorongoro Crater, Tanzania (Höner et al. 2006, 2012). Trends in the size of the Talek West clan (Kenya) between 2008 and 2013 reflected the top-down effects of human disturbance on spotted hyenas. During this time period (2008-2013), livestock grazing inside the Reserve increased more than sixfold, resulting in significantly fewer sightings of lions, which are the top competitor and mortality source of spotted hyenas, after humans. Meanwhile, the Talek West clan increased in size by 95%, eventually reaching 126 individuals and making it the largest spotted hyena clan ever documented (Figure 4.9; Green et al. 2018).

Several studies have investigated ecological correlates of brown hyena density. The highest published densities to date were found in enclosed reserves (Welch & Parker 2016, Edwards et al. 2019), but a substantial proportion of the global population may live outside of protected areas (Kent & Hill 2013). Some studies have documented suppression of brown hyena density by sympatric apex carnivores (e.g., spotted hyenas) through competition (Williams et al. 2021), while others have found brown hyenas and apex carnivores to co-occur at high densities. Co-occurrence could be due to high prey density and divergent foraging strategies (hunting vs. scavenging; Vissia et al. 2021), or because the hunting activity of apex predators creates additional scavenging opportunities for brown hyenas (Yarnell et al. 2013). More work is needed to disentangle the environmental drivers of brown hyena density.

Behavioral studies of individually recognizable hyaenas have allowed researchers to investigate dispersal as well as its potential functions. Spotted hyenas exhibit male-biased dispersal (Höner et al. 2007), but dispersal processes and patterns may vary in different environments. In the Maasai Mara National Reserve, Kenya, most males disperse to new clans from their natal ones, and dispersers seem to experience greater mortality than non-dispersers (Smale et al. 1997), but also more mating opportunities. The reproductive success was compared between philopatric males (i.e., adult natal males who had not yet dispersed) and immigrant males by pairing observational data with genetic samples of known individuals from this study population (Engh et al. 2002, Van Horn et al. 2004, Watts et al. 2011). Engh et al. (2002) reported that, although 20% of the adult males in their study clan were philopatric males, they sired only 3% of cubs born. Thus, the immigrant males had much higher reproductive success than philopatric males who had not dispersed. Engh et al. (2002) also found that immigrant males' reproductive success increased with their length of tenure within the new clan. However, spotted hyenas in the Ngorongoro Crater, Tanzania, exhibited quite a different pattern of dispersal. While the majority of males there dispersed, dispersers and philopatric adult males distributed themselves similarly across clans, electing to join clans with the highest number of potential mates, and attained similar fitness (Davidian et al. 2016). The difference in patterns between these two study sites may reflect either variation in constraints on dispersal or variation in the underlying processes of males' decisions to disperse or not, but further work on known individuals using consistent methodology across study sites is needed to address these hypotheses (Davidian et al. 2016). Collectively, studies of individually recognizable spotted hyenas have revealed that female mate choice drives male-biased dispersal (Smale et al. 1997, Engh et al. 2002, East et al. 2003, Höner et al. 2007, Davidian et al. 2016).

Striped hyenas also seem to be plastic in their dispersal behavior. Califf et al. (2020) compared space-use of known individuals between populations of striped hyenas in central (Laikipia) and southern Kenya (Shompole). Whereas food resources in Laikipia were relatively scarce, they were plentiful in Shompole. Striped hyenas in these two populations showed very different dispersal patterns, with Laikipia females dispersing (Califf et al. 2020) while Shompole females were philopatric (Califf et al. 2020). Females in central Laikipia may have dispersed to avoid competing with close kin for food, whereas the high density of prey in Shompole allowed females to remain near their natal home range (Califf et al. 2020).

Individual identification is particularly critical in studies of social behavior (spotted hyenas, Frank 1986; brown hyenas, Mills 1983a; striped hyenas, Califf et al. 2020; aardwolves, Richardson 1987b, 1991). Repeated behavioral observations of individually recognizable spotted hyenas allow researchers to determine each individual's precise social rank in its clan, and to track ontogenetic changes in individuals' social ranks (Smale et al. 1993, Strauss & Holekamp 2019a). Like many juvenile primates, young spotted hyenas learn their ranks in the clan's dominance hierarchy early in life through a process known as "maternal rank inheritance", where they acquire ranks immediately below those of their mothers, and above those of their older siblings (Holekamp & Smale 1991, Engh et al. 2000). Despite variability in the timing of rank acquisition among juveniles, most young hyenas come to attain the precise rank predicted by the rules of maternal rank inheritance. Nevertheless, transient variation in early-life rank acquisition is associated with long-term fitness consequences; juveniles that "underperformed" at acquiring their expected ranks show reduced survival and lower lifetime reproductive success than better-performing peers, and this relationship was independent of both maternal rank and rank achieved in adulthood (Strauss et al. 2020). In adulthood, rank changes often occur due to passive processes (e.g., births, emigration), but, on rare occasions, they arise from active processes (e.g., rank reversals, Strauss & Holekamp 2019b). That is, individual adult females who repeatedly form coalitions with their top allies may improve their position in the clan's hierarchy, suggesting that social alliances facilitate revolutionary social change. Using lifetime reproductive success as a fitness measure, Strauss & Holekamp (2019b) demonstrated that these status changes can have major fitness consequences. Furthermore, these fitness consequences may increase over multiple generations (Figure 4.10), as small differences in social rank become amplified over time. Thus, knowing each hyena individually allows investigation of rank changes within individuals' lifetimes, as well as the fitness consequences that unfold over many generations.

Camera trapping has scarcely been used to study spotted hyena sociality, but a recent pioneering study (Stratford et al. 2020) suggests that camera traps can be used to shed light on the diversity in group composition and dynamics within this species. Clan size of spotted hyenas is highly variable, ranging from six to over a hundred individuals (Kruuk 1972, Green et al. 2018), depending on environmental factors (Stratford et al. 2020). Extensive direct observations have been used to study the social structures of several large clans of spotted hyenas in grassland ecosystems (Hofer & East 1993, Holekamp & Strauss 2020), where relatively high visibility makes such observations possible. However, direct observations are challenging in dense forests and rugged terrain, so little is known about the social structure of spotted hyenas living in smaller clans in these environments (Stratford et al. 2020). Stratford et al. (2020) demonstrated the utility of camera traps to fill this gap in knowledge using individual identification. They deployed camera traps at waterholes in a Namibian game reserve to capture images of resident hyenas. They used the photographic captures to estimate clan size, assign clan membership, and estimate individuals' connectedness within their clan (Stratford et al. 2020).

Studies of known individual striped hyenas have recently revealed that these animals are not strictly solitary, as previously thought, and that their social behavior varies greatly among populations under different ecological conditions. For example, Califf et al. (2020) found that females in the resource-rich Shompole region exhibited high home range overlap, particularly between kin, whereas those in the resource-poor Laikipia region exhibited no home range overlap. In the Laikipia population, most females' territories were occupied by at least one male (Wagner et al. 2008). In fact, although striped hyenas typically forage solitarily, many studies have observed social aggregations (Wagner 2006, Tichon et al. 2020), particularly at active dens. Alam (2011) observed groups of three to eight striped hyenas gathering at a single den, and cubs from previous litters often helping to rear their younger siblings, sometimes even provisioning them with food (Alam 2011, Mandal 2018). Recently, den-sharing by a pair of closely related female striped hyenas was documented in Shompole (Spagnuolo 2016, Califf et al. 2020).

FUTURE DIRECTIONS IN BASIC RESEARCH

There are countless potential future directions for the role of individual identification in basic research on wild hyenas and aardwolves. Camera traps could be used to expand our knowledge of brown hyenas, striped hyenas, and aardwolves, as well as spotted hyenas inhabiting dense forests and rugged terrain; these are currently poorly understood, especially compared to our knowledge base about the spotted hyena populations inhabiting grassland ecosystems (Dheer et al. 2022). For example, camera traps can be effective at collecting data on the two most elusive hyaenids, striped hyenas and aardwolves, the basic biology of which remain poorly understood. Striped hyenas and aardwolves are nocturnal, persist at low densities, and inhabit rugged terrain, making them difficult to detect. In areas thought to be occupied by residents of these species – based on reported sightings, presence of spoor or scat, or by-catch data from camera trap studies of other species – camera traps can be strategically placed to capture images of striped hyenas or aardwolves (Schuette et al. 2013). That is, camera traps can be systematically distributed on a grid (optionally baited with an attractant) or placed at points of interest, such as waterholes, artificial or natural trails, known dens, or locations where spoor, scat, or direct sightings have been recently reported. If sufficient data can be obtained, then density, space use, movement, and activity patterns could be assessed. For striped hyenas, if the goal is to investigate social group size and composition, fission-fusion dynamics, or social networks, camera traps will likely need to be stationed at active dens, because this species typically forages solitarily but sometimes convenes at dens. These camera traps should be equipped to capture short videos, because higher-quality behavioral data can be extracted from videos than from still images alone.

For all four hyaenid species, more work is needed to delineate ecological drivers of demography and behavior. Studies should collectively cover the diversity of habitats and geographic range of each species. We recommend camera traps for data collection, as these can be used even for elusive populations in dense vegetative cover or rough terrain (Treves et al. 2010, Kelly et al. 2012, Johansson et al. 2020). Similar methods must be used across different studies, so that the findings can be compared or, ideally, eventually incorporated into meta-analyses. These methods can be adapted as needed for the given species or study area, or to meet additional objectives of the research project.

This review presents examples of studies of known individual hyaenids across diverse disciplines, and the possible future directions are equally diverse. We presented several examples of interesting avenues for future research, but the possibilities certainly are not limited to those presented here. Hyena biologists with research foci other than those touched on herein should certainly seek applications that fit their own area of research in the literature, or consider new applications to their interests.

PAST AND PRESENT USE IN CONSERVATION AND MANAGEMENT

Individual identification of hyaenids facilitates research that informs conservation and management of free-living populations. First, individual identification has been employed to develop methods for density estimation that are far superior to traditional methods (Karanth & Nichols 1998, Treves et al. 2010, Kelly et al. 2012, Green et al. 2020, Vissia et al. 2021). Population density is critical information needed for wildlife conservation (Rich et al. 2019), and the IUCN has identified estimation of population size as a top research priority for conservation of all four hyaenid species (AbiSaid & Dloniak 2015, Bohm & Höner 2015, Green 2015, Wiesel 2015). Photographic capture-recapture methods have been used to estimate density of hyaenid populations, even for rare or elusive hyaenids (O'Brien & Kinnaird 2011, Alam et al. 2015, Edwards et al. 2019, Vitale et al. 2020, Braczkowski et al. 2022) and those occupying areas only accessible to researchers on foot (Henschel et al. 2014). Accurate estimates of density are important as this allows for better estimation of global population size and the designation of appropriate conservation status (Akçakaya et al. 2006).

Second, information on hyaenids' social systems gleaned from studies of known individuals may also be useful in conservation planning. Camera trap (Mandal 2018, Tichon et al. 2020) and observational studies (Frank 1986) form the basis of much of our understanding of social grouping, which may inform density estimation. This body of research has also provided evidence of cooperative breeding in brown hyenas (Mills 1990) and, more recently, in striped hyenas (Alam 2011, Spagnuolo 2016, Mandal 2018, Califf et al. 2020). This knowledge may help to predict how reduced social group sizes (resulting from declines in population density) may affect reproductive success in cooperatively breeding populations (van der Meer et al. 2013, Tichon et al. 2020).

Our knowledge of population connectivity has benefited from direct observations of spotted hyenas bearing unique natural markings, sometimes paired with complementary data from radio collars, GPS collars, or genetic samples. The resultant findings have illuminated patterns of space use and movement, including natal dispersal (Smale 1997, Boydston et al. 2005), and reproductive success in spotted hyenas (Engh et al. 2002, Watts et al. 2011). Gene flow among spotted hyena clans may have important implications for metapopulation persistence (McCullough 1996, Hanski & Simberloff 1997, Dolrenry et al. 2014).

Finally, individual identification of hyaenids can be used to investigate their role within the ecosystem, to the benefit of multiple species. Ongoing research into predictors of demographic parameters identifies components of suitable habitat and threats to hyaenid population persistence (Singh et al. 2010, 2014, Mandal 2018), which may be directly targeted by conservation efforts. Camera traps can be used to monitor multiple species within the same study area (Kelly et al. 2012, Green et al. 2020). Illumination of the dynamics within large carnivore guilds, as well as the ecological relationships among carnivores and their wild and domestic prey (Green et al. 2018), may enable scientists and practitioners to foresee the consequences of changes within one species or trophic level for other sympatric species. Spotted hyena movement may also shed light on impending shifts in the sympatric large carnivore community; Green et al. (2019) found that, within spotted hyena territories, the areas frequented by low-ranking (rather than high-ranking) hyenas and in which hyenas moved at the highest speeds exhibited declines in carnivore species richness in the following months. The spatial resolution of this analysis was small (200 x 200 m cells), much smaller than a large carnivore’s home range, so this may reflect changes in space use by sympatric carnivores rather than their density in the study area. More research is needed to explore this relationship, to unravel the underlying mechanisms, and to determine appropriate applications to conservation and management.

FUTURE DIRECTIONS IN CONSERVATION AND MANAGEMENT

Many practical applications of individual identification of hyaenids remain unexplored. One potential application is the identification of population sinks. Source-sink theory posits that average fitness varies across subpopulations within a metapopulation due to variable habitat quality. Subpopulations inhabiting patches of high-quality habitat (source populations) are expected to experience high fitness, thus producing a surplus of individuals, while subpopulations inhabiting poor-quality habitats (sink populations) experience low fitness, with mortality exceeding local recruitment, resulting in a population deficit (Pulliam 1988, Kristan 2003, van der Meer et al. 2015, Kelt et al. 2019). Population sinks are maintained by immigration from source populations (Pulliam 1988). A common example of source-sink dynamics in large carnivores is edge effects on populations in protected areas; that is, conflict with humans along the boundaries of protected areas often turns border areas into population sinks, with populations in core areas acting as sources (Woodroffe & Ginsberg 1998, Balme et al. 2010). Knowledge of edge effects have been used to improve conservation and management of leopards in South Africa, potentially to the benefit of other carnivores, including spotted hyenas (Balme et al. 2010). Several studies have found evidence of edge effects on probability of population persistence (Woodroffe an&d Ginsberg 1998) and mortality (Newmark 2008, Pangle & Holekamp 2010) of spotted hyenas, but there is still much work to do in this area.

More urgently, we encourage researchers to take advantage of hyaenids' unique natural markings to identify ecological traps. An ecological trap represents an extreme case of a population sink, in which the animals actually prefer the sink to the source area (Gates & Gysel

1978, Delibes et al. 2001, Donovan & Thompson 2001). Under classical source-sink theory, it is assumed that animals can accurately assess habitat quality and therefore prefer source habitat, only immigrating to sink habitat when the source habitat is already occupied. When vacancies become available in the source area, individuals should emigrate from the sink to the source (Kristan 2003, Kelt et al. 2019). Through continuous density-dependent immigration, sources and sinks can persist. In fact, sink patches may contribute to the persistence of the metapopulation as a whole (Pulliam 1988, Howe et al. 1991, Kelt et al. 2019). However, when environmental cues are uncoupled from true habitat quality – most often through anthropogenic disturbance – a population sink may become more attractive to animals than nearby source areas, representing an ecological trap (Gates & Gysel 1978, Delibes et al. 2001, Donovan & Thompson 2001). Elevated mortality rates in ecological traps create vacancies that invite immigration from nearby source populations, creating a "vacuum effect" that can lead to extirpation of the entire metapopulation over time (Balme et al. 2010). Occupancy and density data alone are insufficient to identify population sinks and ecological traps (Kelt et al. 2019). Rather, the relationship between habitat preference and habitat quality must be delineated, for example, using data on fecundity, mortality, and dispersal over time (Pulliam 1988, Kelt et al. 2019). Empirical evidence of ecological traps has been found for other large carnivores (van der Meer et al. 2013, 2015, Lamb et al. 2017), but we are unaware of any research on ecological traps for hyaenids specifically. In the face of continuing anthropogenic change, ecological traps may become increasingly widespread threats to the persistence of large carnivore populations (Balme et al. 2010). This could certainly be the case for hyenas, which could potentially be attracted to human settlements (e.g., by livestock, crops, or refuse; Kruuk 1976, Kolowski & Holekamp 2008, Kissui et al. 2019). Conservation planning should incorporate identification of and differentiation between conventional population sinks and ecological traps (van der Meer et al. 2015).

Increasing anthropogenic disturbance presents many natural opportunities to assess the responses of hyaenids to human activity. Monitoring efforts should be initiated in areas subject to imminent increases in anthropogenic activity, such as livestock grazing or tourist visitation, to provide baseline data. These efforts – whether direct behavioral observations or camera trap studies – can run continuously or be repeated at future time points using the same methods each time to quantify demographic or behavioral changes that occur alongside changing levels of human disturbance. This same process could also be applied to sites targeted for restoration or at which prohibitions against human activities are newly enforced to assess resilience of hyaenid populations. The COVID-19 pandemic presented another natural "experiment," because travel restrictions interrupted ecotourism. In many countries, pre-pandemic data could be compared to data collected after the imposition of travel restrictions to investigate effects of tourism on hyaenids. Anthropogenic removal of sympatric carnivores or natural prey could allow researchers to delineate demographic and behavioral responses to reduction of apex carnivores (Green et al. 2018), mesocarnivores, or prey.

Identification of problem animals (Linnell et al. 1999) represents another potential future direction for applied research on individually identifiable spotted hyenas. Livestock depredation imposes a financial burden on affected households and can prompt retaliatory killings of hyenas and sympatric carnivores (Kissui 2008). Although we are unaware of any studies that sought to determine whether livestock depredation is attributable to a subset of problem animals, previous research on intrapopulation variation in hyaenid behavior suggests that this is likely. First, socioecological conditions affect space use in spotted hyenas, putting some individuals at higher risk of conflict with humans. In the Maasai Mara National Reserve, Kenya, low-ranking females without den-dependent cubs maintain the largest home ranges of any adult females, particularly in times of prey scarcity (Boydston et al. 2003, Green et al. 2019). Upon reaching puberty, males begin making exploratory forays beyond the boundaries of their territory, and adult males maintain larger home ranges than their female clanmates, venturing three to four times as far from the center of their territory as females (Boydston et al. 2005). Thus, males and low-ranking females may be more likely to venture into human-disturbed landscapes than high-ranking females, and thus experience an elevated risk of human-caused mortality.

Second, hyena personalities may affect individuals' likelihoods of engaging in conflict with humans. Animal personality refers to individual variation in behavioral traits such as boldness, neophobia, and exploration that is consistent across time and context (Yoshida et al. 2016, Greenberg & Holekamp 2017, Turner et al. 2020). Individual personalities converge to affect population responses to novel environmental conditions, such as human disturbance (Merrick & Koprowski 2017). Greenberg and Holekamp (2017) and Turner et al. (2020) found that spotted hyenas from highly human-disturbed areas were less bold, less neophobic, and more exploratory than those in areas of low human disturbance. Boldness was negatively correlated with survivorship to adulthood in populations exposed to both low and high human disturbance. The relationships among intrapopulation variation in behavioral traits (personality) and space use have yet to be empirically studied in the context of human-hyena conflict.

If livestock depredation varies among individual spotted hyenas, one would also expect to observe intrapopulation variation in selection of native prey. Currently, the strength of individual diet specialization is poorly understood in hyaenids. This could be investigated through behavioral observations of hunting and feeding of known individuals or by analyzing tissue samples or repeat scat samples from known individuals. However, most published studies of scat analyses in hyenas used scat from unknown individuals (Henschel & Skinner 1990, Abay et al. 2011, Yirga et al. 2013), hindering the study of dietary specialization in hyaenids.

Intrapopulation variation in encounter rates with livestock affects livestock depredation risk and represents another exciting frontier in human-hyena conflict mitigation. For example, a camera trap grid could be placed to cover a mosaic of areas of livestock use (e.g., livestock corrals) and non-use, large enough to encapsulate at least one entire spotted hyena clan territory. Network analyses can be used to identify clans (Vitale et al. 2020), and clan membership can be paired with locations of photographic capture events to delineate territory boundaries. The camera trap data could be analyzed in a spatially explicit capture-recapture framework to estimate the size of a clan whose entire territory is included within the camera trap array and encompasses livestock corrals. Observers could then determine the number of visits to livestock corrals by each individual hyena. Variation in corral visit frequency would likely reveal differences in individuals' tendencies to pass through these areas, representing individual-level differences in encounter rate with livestock. We are unaware of any camera trap studies at livestock corrals or grazing areas that differentiate among individual hyenas. In fact, we are only aware of one study in which camera traps were deployed at livestock corrals (Hoffmann et al. 2022). In this study, Hoffmann et al. (2022) used camera trap data to quantify encounter and attack rates at the species level but did not distinguish among individuals of each species. Innovative research methods are worthy of exploration, as are analytical applications to investigate human-hyena interactions and dynamics in shared landscapes.

Resources for conflict mitigation are limited, so identification of high-conflict areas is essential. Hyenas who frequent human settlements are likely at a higher risk of human-induced mortality (e.g., spearing, poison, snares) than others, regardless of their interactions with livestock. Individual-level space use and mortality data from known hyenas could be useful in identifying age-sex class and rank of hyenas at the highest risk of human-caused mortality. Furthermore, by identifying which high-use areas are correlated with the highest hyena mortality rates, efforts to reduce human-hyena conflict could be concentrated where they are most needed.

CURRENT LIMITATIONS

Despite its advantages, there are some drawbacks to individual identification using natural markings. To demonstrate these points, we draw from examples of hyaenids. There are certainly limitations of other methods discussed herein, such as camera trapping (Green et al. 2020, Dheer et al. 2022), but here we specifically focus on the limitations of individual identification of hyaenids in both camera trap studies and direct observations.

Using naturally-occurring markings to identify individuals can be time-consuming and is not always reliable. For example, one study tested agreement among observers in individual identification of striped hyenas from camera trap images through a double-blind experiment in which three independent observers identified hyenas in 26 photographic captures (Harihar et al. 2010), following methods of Kelly et al. (2008). All three observers only agreed on the identity of the hyena for 76.80% of the capture events (Harihar et al. 2010).

According to Johansson et al. (2020), each time an attempt is made to identify an individual, there are five possible outcomes: correct identification, a splitting error, a combination error, a shifting error, or exclusion of the datum. A splitting error occurs when the focal individual is already present in the dataset but is mistakenly identified as a new individual. A combination error occurs when the focal individual has not yet been observed but is mistaken for a different animal that has already been observed. A shifting error occurs when the focal individual has already been observed and is mistaken for a different individual, who has also already been observed. Finally, a datum may be deemed unusable and excluded from the dataset either correctly (true exclusion) or erroneously (exclusion error). A true exclusion occurs when identification is truly infeasible, for example, due to poor lighting or blockage of the observer's view by features of the environment (e.g., tall grass) or another animal (Kelly et al. 2008, Harihar et al. 2010). An exclusion error occurs when sufficient information is available to make the identification, but the observer fails to identify the individual (Johansson et al. 2020).

Identification errors can skew the results of the studies in which they occur. In estimation of population size or density, splitting errors lead to overestimation, whereas combination errors lead to underestimation (Johansson et al. 2020). Shifting and exclusion errors do not necessarily bias the results of traditional capture-recapture analyses but shifting errors are problematic in spatially explicit capture-recapture analyses (Johansson et al. 2020). In a camera trap study of 16 snow leopards, photographic captures had an 8.70% probability of being excluded from the dataset. Of the remaining photographic captures, the probability of splitting errors (9.10%) was far higher than that of combination or shifting errors, leading to an overall misidentification rate of 12.50% (Johansson et al. 2020). The prevalence of splitting errors ultimately inflated the estimated population size by about one third (Johansson et al. 2020). Population estimates are central to conservation and management planning, and overestimation of population size may potentially undermine conservation efforts (Choo et al. 2020, Johansson et al. 2020). Splitting errors may be the most pervasive error type and are especially problematic in studies of threatened and endangered species, but more studies of identification error are needed to better understand the prevalence of error types across species with distinct individual natural markings. The other types of error (combination, shifting, and exclusion) also have the potential to bias estimates of demographic parameters, specifically if they are not randomly distributed across the population (Johansson et al. 2020), such as if some age-sex classes are more difficult to identify than others. For example, subadult spotted hyenas go through a phase in which they become very fluffy, making their spot patterns difficult to see. Additionally, ear damage and scars accumulate over a hyena's lifetime, and are therefore relatively uncommon in young hyenas. On extremely old hyenas, on the other hand, spots may fade. For these reasons, it may be easier to identify middle-aged hyenas than those that are very young or very old. In addition to yielding erroneous population estimates (Johansson et al. 2020), misidentification can obscure the results of behavioral or genomic studies.

Standards for reporting methods and accuracy of individual identification are severely lacking. Most studies do not describe the methods they used to avoid misidentification, provide photographic evidence that individuals can be differentiated, or quantify the error rates of identification, thus precluding reviewers and readers from critically assessing the studies' reliability and robustness (Choo et al. 2020). In summary, the methods by which data on known individuals are collected, analyzed, and reported certainly need further development. This is not to say that we should not use individual identification, but rather to stress the importance of quantifying, rectifying, and reporting errors, as well as refining methods for managing interobserver discrepancies and unclassifiable capture events (Choo et al. 2020, Johansson et al. 2020).

FUTURE DIRECTIONS IN METHODOLOGY

Many of the current limitations of individual identification represent potential targets for methodological improvements. These include observer training, testing for errors, error prevention, transparency and accountability in reporting, and software to aid observers in identification. We also suggest methods by which the resultant data could be used to improve parameter estimation and answer novel questions.

More information is needed to determine what specific training or experience decreases observers’ misidentification rates. Virtual training tools, such as that recently produced for photographic identification of snow leopards (Johansson 2020), may be helpful in improving training as well as in testing identification error. By testing rates of specific error types, targeted training approaches and identification methods can be identified to avoid the common error types (Choo et al. 2020, Johansson et al. 2020). Johansson et al. (2020) suggested prioritization of verification of new individuals, based on the prevalence of splitting errors. When feasible, multiple independent observers should identify individual animals (Choo et al. 2020, Johansson et al. 2020), and methods for resolving disagreement among observers and management of images deemed unclassifiable should be carefully chosen (Choo et al. 2020, Johansson et al. 2020). Using multiple independent observers not only helps to detect and rectify identification errors but allows authors to report rates of interobserver agreement. Even when errors cannot be effectively rectified, quantification of error rates can allow for selection or development of modeling approaches that minimize the impacts of these errors on the results (Yoshizaki et al. 2009, Mendoza et al. 2011, Johanssson et al. 2020). To achieve higher transparency and accountability in reporting, we recommend following the Individual Identification Reporting Checklist presented by Choo et al. (2020).

Software programs to automate individual identification have been successfully applied to multiple mammal species (Bolger et al. 2012, Crall et al. 2013, Schneider et al. 2019, Choo et al. 2020), and could potentially be applicable to hyaenids in the future. Computer vision has been used to assist manual identification by human observers in other carnivores with distinct coat patterns, such as cheetahs (*Acinonyx jubatus*, Kelly 2001), tigers (Hiby et al. 2009), and bobcats (*Lynx rufus*, Mendoza et al. 2011). A computer-aided approach relies on a human observer to confirm the final classification, but can reduce the man-hours needed to process large datasets (Kelly 2001) and reduce rates of misidentification (Hiby et al. 2009, Mendoza et al. 2011). Automated identification methods are currently underdeveloped and face many of the same challenges that human observers do (e.g., poor image quality, camera angle, Johansson et al. 2020). However, with further development, these methods could become highly effective and widely used in the future (Schneider et al. 2019). We are unaware of any studies that have used automatic methods to identify individual hyaenids, but suspect that this would be difficult, especially in species whose patterns are especially prone to distortion, such as by shifting position of long fur (spotted and striped hyenas) or due to camera angle (brown hyenas).

Data from individually identifiable animals can be applied to improve model parameter estimation. Counterintuitively, although studies of occupancy do not require differentiation of individuals, they could still benefit from examination of unique markings. Individual identity may be useful in determining whether or not the assumptions of spatial independence and population closure have been met (Edwards et al. 2018). Additionally, further research on personality may better inform estimates of detection probability for hyaenids. This research by definition requires individual hyaenids to be identified and studied across time and context.

New research questions may be addressable by combining multiple data types. Individually recognizable animals can be studied by pairing visual observations (direct or through photos) with data collected with either noninvasive (Table 4.1) or invasive (radio-collars, Stratford et al. 2020, Edwards et al. 2020; biosamples, Engh et al. 2002, Van Horn et al. 2004, Watts et al. 2011) methods. Additionally, experts could visually identify individuals in geotagged photos of sufficient quality submitted by local people or tourists. There are also many large datasets of existing images produced by camera trap studies that could be used to answer new research questions. Thus, advances in methodology of individual hyaenid identification could facilitate citizen science and new collaborations.

The most vocal hyaenids, spotted hyenas, may be individually distinguishable not only through visual identification, but possibly through acoustic identification as well (Lehmann et al. 2022). Spotted hyenas' loudest vocalizations, called "whoops," are emitted in bouts and can be heard from up to five kilometers away (Kruuk 1972, East and Hofer 1991a). Whooping serves important functions, such as recruiting clanmates to cooperate in defense of a shared resource, and are used in various contexts to transmit information about the callers' location, age, sex, affective state, and, importantly, identity (East & Hofer 1991a, East & Hofer 1991b, Theis et al. 2007, Benson-Amram et al. 2011, Gersick et al. 2015, Lehmann 2020). Acoustic variation among different individuals (signal strength) and consistency of individuals' acoustic signatures over time (signal stability) are necessary for acoustic identification of individuals (AIID; Linhart et al. 2022). If the acoustic variation quantified by Lehmann et al. (2022) proves to be consistent over time, as suggested by East and Hofer (1991a), then AIID could become a powerful tool for studying spotted hyenas.

Vocalizations may be collected through focal or passive recording. In focal recording, an observer typically uses a handheld microphone and digital recorder. In passive recording, vocalizations are captured by autonomous recording units (ARUs) placed in the animal's environment. Focal recording has many benefits, such as yielding high-quality samples and allowing the observer to record the emitter's identity, the emitter's posture and orientation in relation to the microphone, the distance between the emitter and the microphone, and contextual information. However, focal recording is much more time consuming than passive recording. Using focal recordings for AIID in a capture-recapture framework is important for feature selection and external validation, and can be treated as a pilot study, with the ultimate goal of developing methods for AIID using passive recording (Linhart et al. 2022). We are unaware of any work that has identified individual hyenas based on passive recording, but this could be an interesting area for future exploration. Next steps should include developing software to perform AIID through machine learning and to externally validate the results. Additionally, the maximum distance at which a whoop can be correctly assigned to the emitter should be determined. These steps all require pilot data from focal recordings. If whoops can be recorded from kilometes away and the emitter accurately identified, then an ARU could potentially obtain much more data than a camera trap placed at the same location.

CONCLUSIONS

The unique markings of hyaenids are indispensable in ongoing research and have greatly enhanced our understanding of these species. We have highlighted several interesting studies that exemplify this, but this is by no means a comprehensive review of the literature built on individual identification of hyaenids. In addition to the fields discussed here, this method has facilitated studies of hyena cognition (Johnson-Ulrich et al. 2020), disease ecology (Höner et al. 2012, Gering et al. 2020), mate choice (Engh et al. 2002, Szykman et al. 2001), behavioral endocrinology (Dloniak et al. 2006, Montgomery et al. 2022), and microbiota (Theis et al. 2013, Rojas et al. 2020), among many others. Comparative work within the family Hyaenidae is especially useful, as the socioecological diversity within this family allows investigation of the evolution of various traits in closely related species and has been particularly useful in studies of social evolution and intelligence (Holekamp 2007, Holekamp et al. 2007, Holekamp & Benson-

Amram 2017, Johnson-Ulrich 2017). Applied work with hyenas *in situ* is timely and important for protecting human livelihoods from crop raiding and livestock depredation, and for conserving rare striped and brown hyenas. Furthermore, results of such studies may help to inform conservation and management of other large mammalian carnivores or even whole ecosystems (Green et al. 2019).

Despite the wealth of knowledge about spotted hyenas, many unanswered questions remain, and relatively little is known about the other hyaenid species, especially striped hyenas. We have identified several of the many gaps in our current understanding that can be answered using studies of free-living, individually recognizable hyenas or aardwolves. Furthermore, identification by natural markings has been combined with other methods to generate novel datasets. For example, some studies have fitted subjects with collars to aid in visual identification or location of subjects for repeated behavioral observations, or to supplement data from direct observations with spatial data from GPS collars, while also using coat patterns to differentiate individuals (Richardson 1987a, 1987b, 1991, Silwa 1996, Boydston et al. 2003, Califf et al. 2020). Individually known subjects may also be captured to obtain biosamples to complement behavioral data (Höner et al. 2007, Califf et al. 2020). Identification by natural markings has also been combined with various noninvasive methods (Table 4.1) to produce complementary datasets. Many possible combinations of methods have yet to be used for hyenas, such as pairing camera traps with hair snares or identifying prey hair or DNA in scat from known individuals to study individual diet variation and specialization (Larson et al. 2020). Noninvasive methods are unlikely to replace invasive methods completely, but they can be beneficial for minimizing stress and risk of injury to the animals, circumventing logistical limitations (including obtaining permits) and trap shyness, maximizing sample size, and detecting elusive species (Kelly et al. 2012).

Noninvasive individual identification has proven critical to building our understanding of the demography, social behavior, reproduction, and ecology of wild hyenas and aardwolves. The literature reviewed herein was selected to showcase the value of this method and to showcase the diversity of its applications, but we merely scratch the surface of this vast body of work. We encourage researchers and conservation practitioners to seek out papers that describe the use of this method in their own areas of interest and to consider how their current or future projects may benefit from incorporation of individual identification of study animals. Researchers already using individual identification should strive to meet the criteria specified in the Individual Identification Reporting Checklist (Choo et al. 2020). Besides the large body of published work to date, there are certainly many unexplored uses of individual identification. Researchers should consider new applications of this method to address basic research questions and methodological advances to address the limitations discussed above. Importantly, there are many avenues of applied research that have gone largely unpursued to date in hyenas, including identification of problem animals in livestock and crop damage. We encourage creative fusions of methods and the application of individual identification to basic and applied research questions. The methods we have discussed should be useful in future studies of wild hyaenids, as well as other mammalian carnivores, by facilitating new research, improving reliability and transparency of published work, and informing conservation and management strategies.

TABLES

Table 4.1

Creative combinations of methods used with spotted hyenas have allowed researchers to collect biological samples noninvasively from known individuals to pair with direct observations. Here, we report methods paired with direct behavioral observations, the type of complementary data yielded by this method, and citations of researchers who have successfully employed this fusion.

Method(s)	**Data type**	**Citation(s)**
Opportunistically pluck cubs’ hairs Necropsies of dead hyenas	Genetic	Höner et al. 2007
Feces collection	Genetic	Watts et al. 2011
Feces collection	Hormones	Dloniak et al. 2006; Van Meter et al. 2008, 2009
Sampling by saliva stick	Hormones	Montgomery et al. 2022
Feces collection	Microbiome	Rojas et al. 2020

FIGURES

Figure 4.1

Shown here are reference photographs of two different hyenas in the Maasai Mara National Reserve, captured on different occasions: a female named Pike (a, b, c, d) and a male named Kaikura (e, f). Contrast, brightness, and sharpness were edited to enhance visibility of spots. Spotted hyenas’ spots are not bilaterally symmetrical, so reference photographs should ideally include both sides. Spots from multiple body parts should be used, but the specific parts used may depend on visibility.

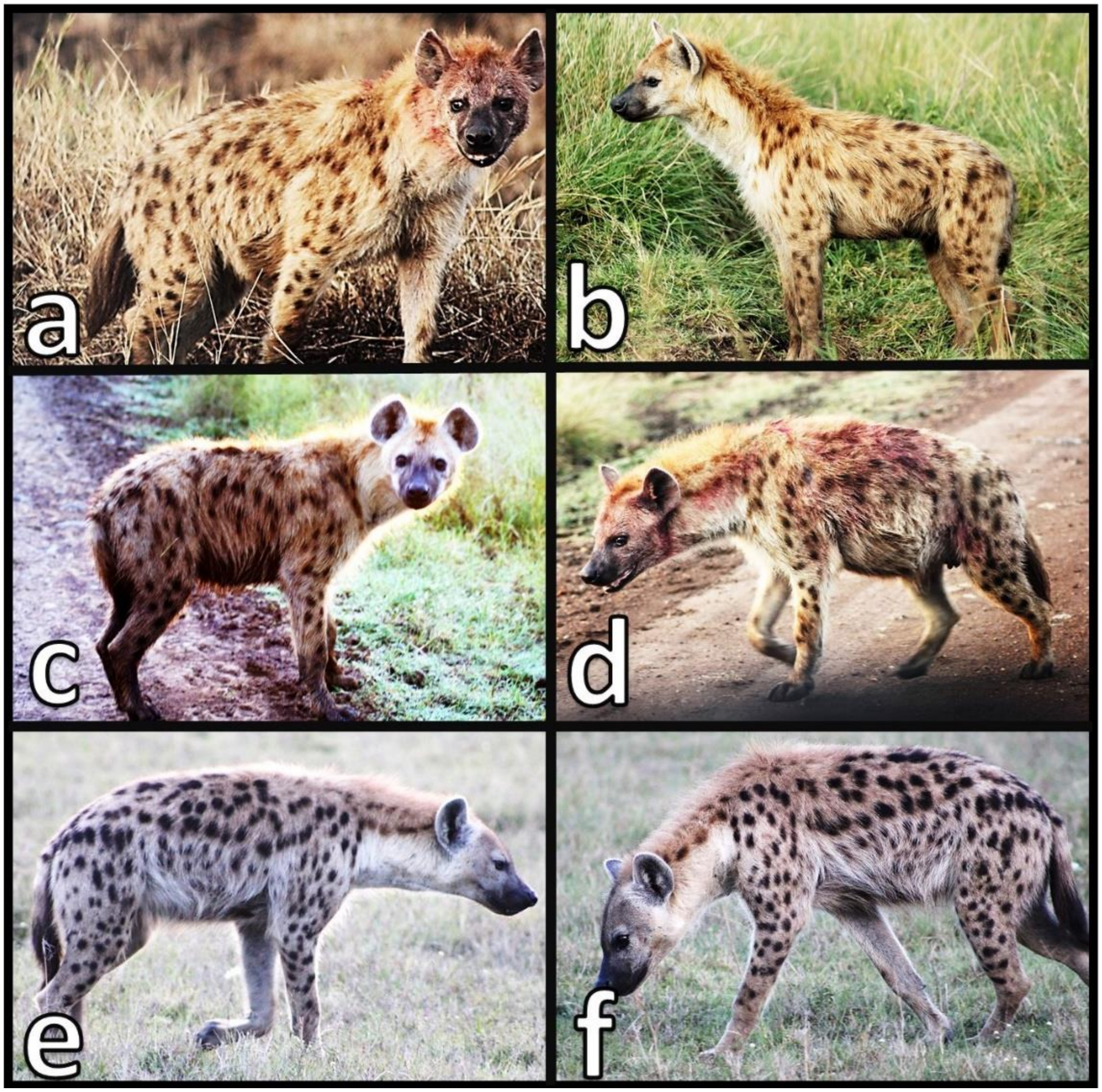


Figure 4.2

(a) A photo album of one of the Mara Hyena Project’s study clans in the Mara Triangle, Kenya. The photo album is organized by age-sex class. These photos are updated throughout the hyenas’ lifetimes, and each photo is marked with the date taken. The position and shape of each hyena’s ear damage, if present, are noted on reference photos. Whereas a hyena’s spots never change, ear damage often varies over a hyena’s lifetime. Therefore, ear damage should be used to narrow the list of likely candidates, but final confirmation should always rely on spot patterns. (b) Ears of eight different spotted hyenas in the Mara Triangle, Kenya. Ear damage is acquired while fighting with conspecifics or other large carnivores. Photo credit for (a) to Erin Person.

Figure 4.3

Distinct ear damage on a spotted hyena cub with its natal coat. This cub, Black Bear, was the only cub at this communal den with a slit on this part of its ear (indicated by white arrow), so he could be clearly distinguished from the other cubs, including his littermate. This allowed researchers to identify Black Bear before he shed his black natal coat and developed spots.

Figure 4.4

A natural ear notch on the right ear of the same brown hyena at the ages of five (a) and 15 years (b). The shape of the original notch has changed, and new smaller notches have appeared over time.

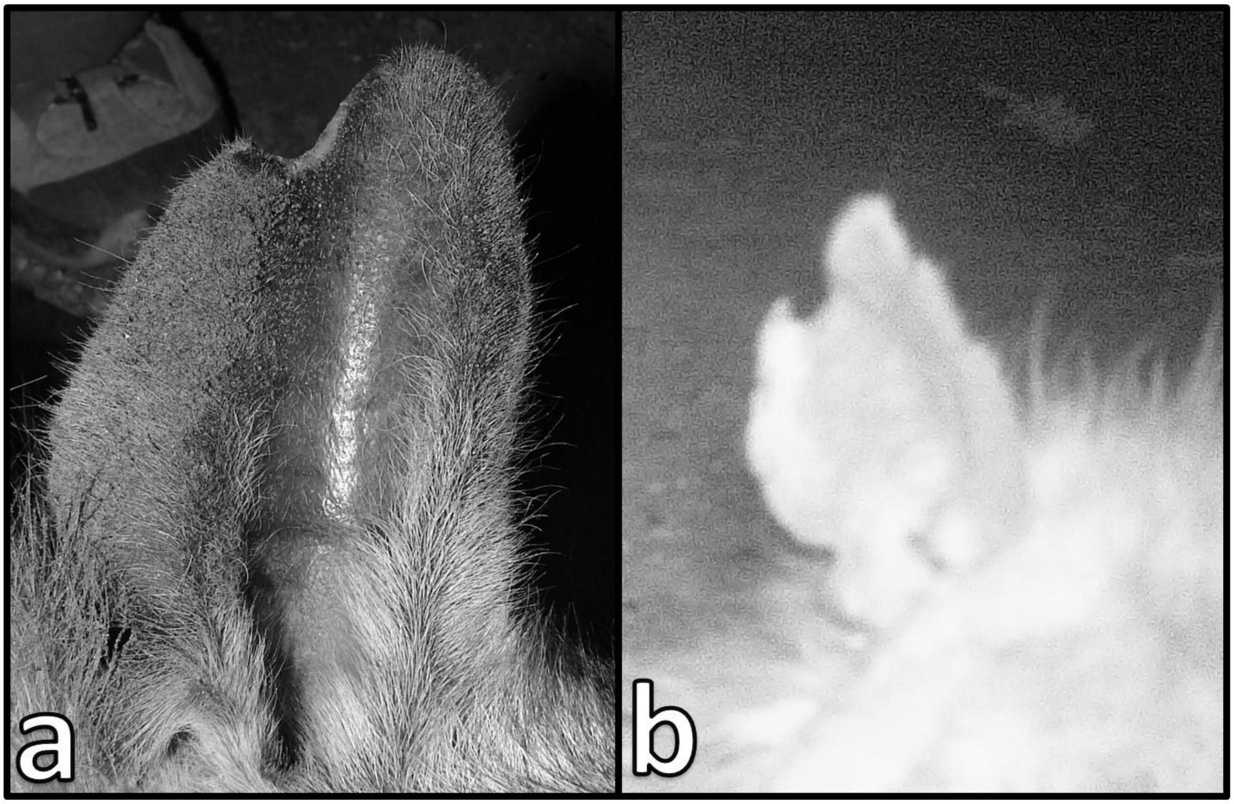


Figure 4.5

The top row (a-c) shows the anterior surfaces of the forelegs of a male brown hyena named Kai-Alex, and the bottom row (d-f) shows those of a second male, Lloyd. Kai-Alex's leg stripes are the same at six months (a) and 2.5 years of age (right foreleg, b; left foreleg, c). Similarly, Lloyd's foreleg stripes are consistent from cubhood (d) to adulthood (right foreleg, e; left foreleg, f). Photos of leg stripes at 2.5 years of age were taken while hyenas were anesthetized.

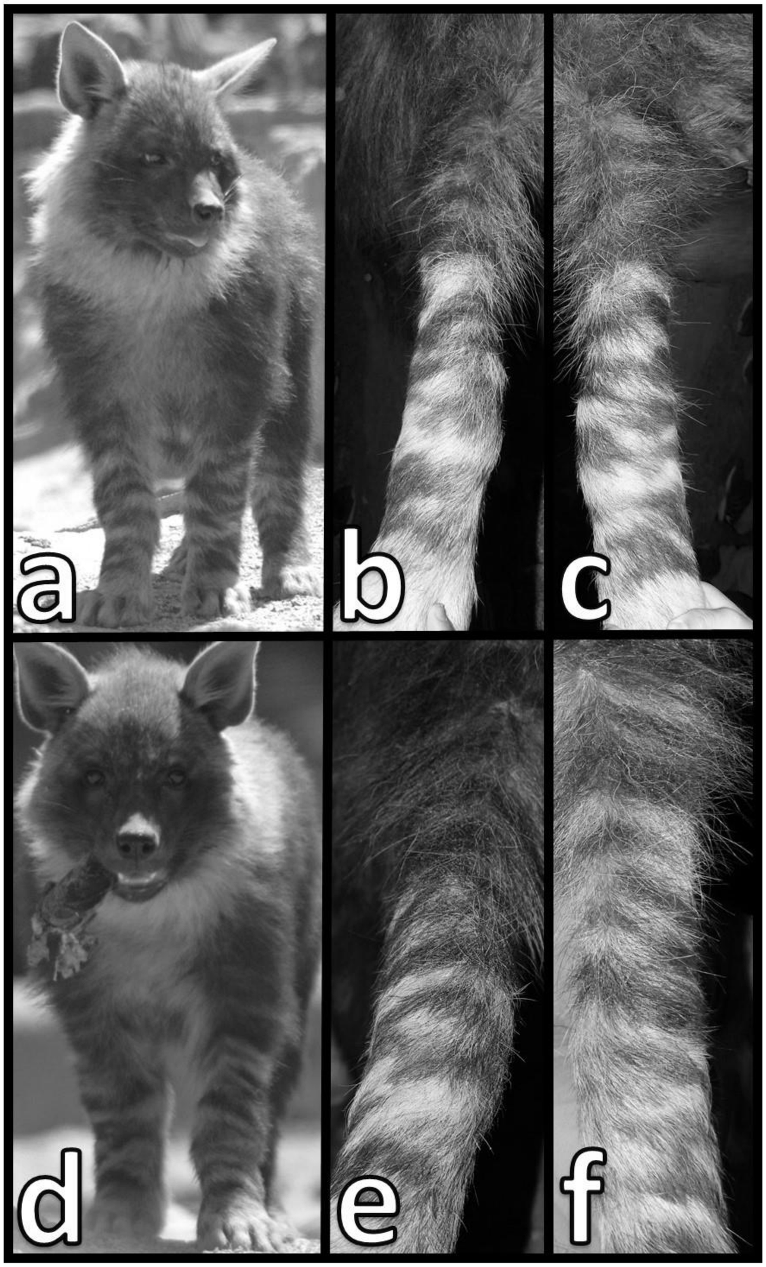


Figure 4.6

A single female brown hyena, Alaika, is shown at the ages of five, eight, and 12 years. The first frame (a) shows the lateral view of Alaika's right foreleg at five (left), eight (center), and 12 (right) years of age. We can see that the stripes are consistent over her lifetime. In the second frame (b), we see that the anterior view of the right foreleg looks quite different from the lateral view of the same leg, but, again, the stripes are consistent throughout her lifetime (five years of age, left; eight years, center; 12 years, right). Photographs in (a) and (b) were taken while Alaika was anesthetized for handling on three different occasions. (c) shows remote camera trap images of Alaika with sufficient clarity to identify her using lateral stripes of right foreleg (left, center), and insufficient clarity for confident identification (right).

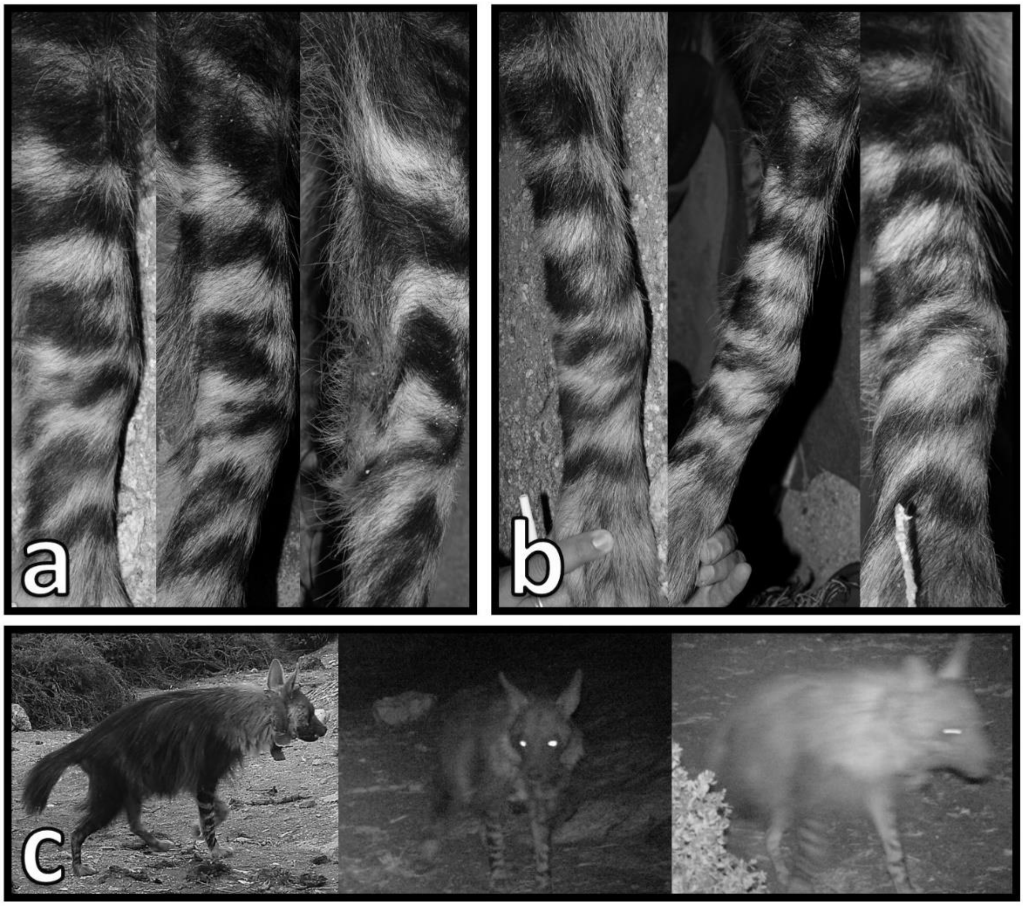


Figure 4.7

Left sides of two known striped hyenas in a population near Shompole, Kenya, captured on different occasions: male M113 (a, b) and male M114 (c, d). M113’s mane is erect in (a), revealing some stripes on his left flank, but is not erect in (b), thus partially covering and distorting these stripes. Markings on the fore- and hindquarters are more useful than the flanks for identification of striped hyenas. In this population, many hyenas have a single solid stripe over a double stripe on their left hip (white boxes; a, c). As an observer becomes more experienced identifying subjects in a given population, they should recognize interindividual similarities such as this and focus on more variable features. Therefore, slight similarities among hyenas should not necessarily lead to a reduction in accuracy, particularly if observers use patterns from multiple body parts to confirm each identification. Photo credit to Aaron Wagner.

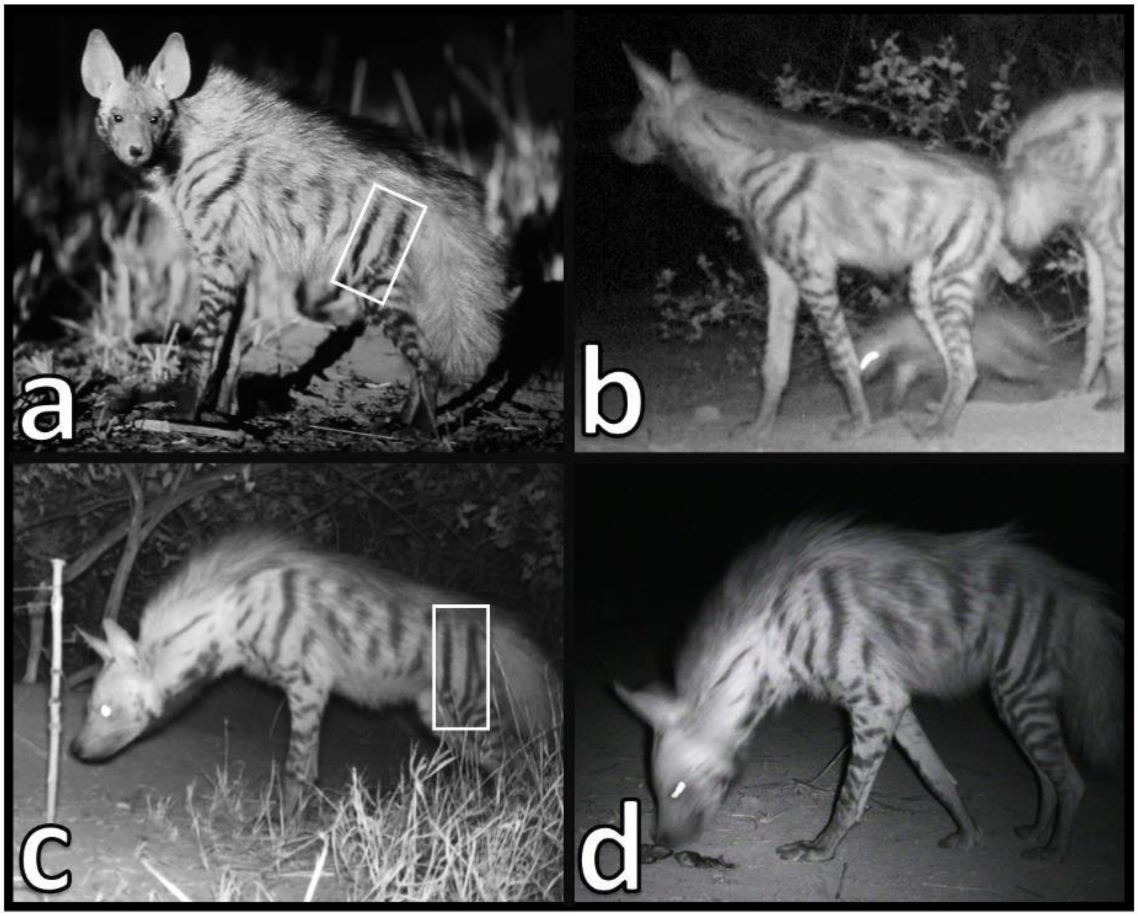


Figure 4.8

Incidental photographic captures of aardwolves by remote camera traps used by the Brown Hyena Research Project in Namibia. (a) and (b) show two captures of the same individual, viewed from different angles. (c) shows a second individual. These two individuals can be easily distinguished by the stripes on their shoulders. While individuals can often be recognized even when viewed from different angles, applying bait or taking advantage of natural or manmade trails can help position animals relative to the camera lens for optimal visibility.

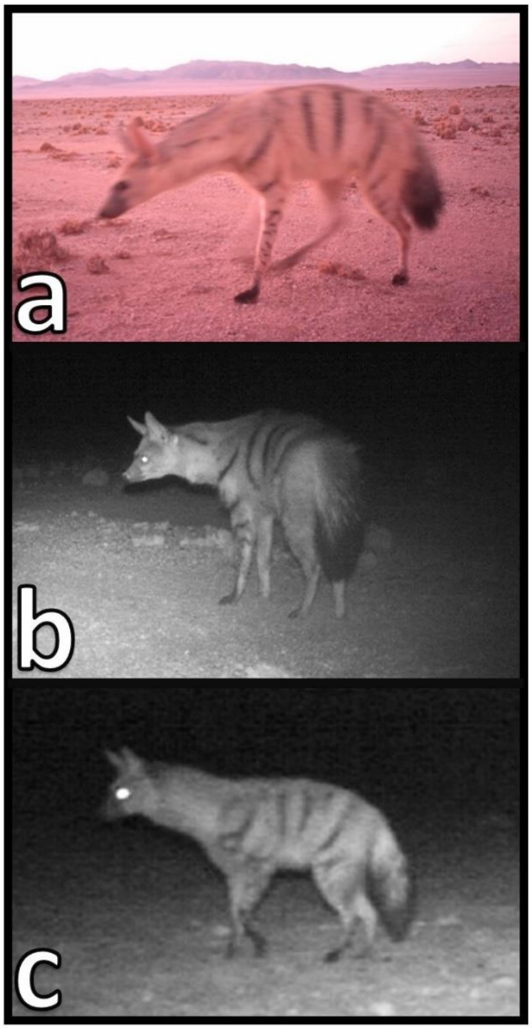


Figure 4.9

Variation over time in the sizes of six study clans in the Maasai Mara National Reserve, Kenya. For each time point, the annual mean clan size is shown (with standard error bars when multiple population counts were performed within the given year). Data for each of six study clans, represented by symbols indicated in the key at the top left, were included from the first year each was studied through 2013. The Talek West clan split into two daughter clans in both 1989 and 2000, indicated by horizontal black bars over the data points. Each of these two clan fissions resulted in a reduction in size of the parent clan, as a subset of this clan's members left to form a new clan in each case. Reproduced from Green et al. (2018) with permission from *Biodiversity and Conservation.*

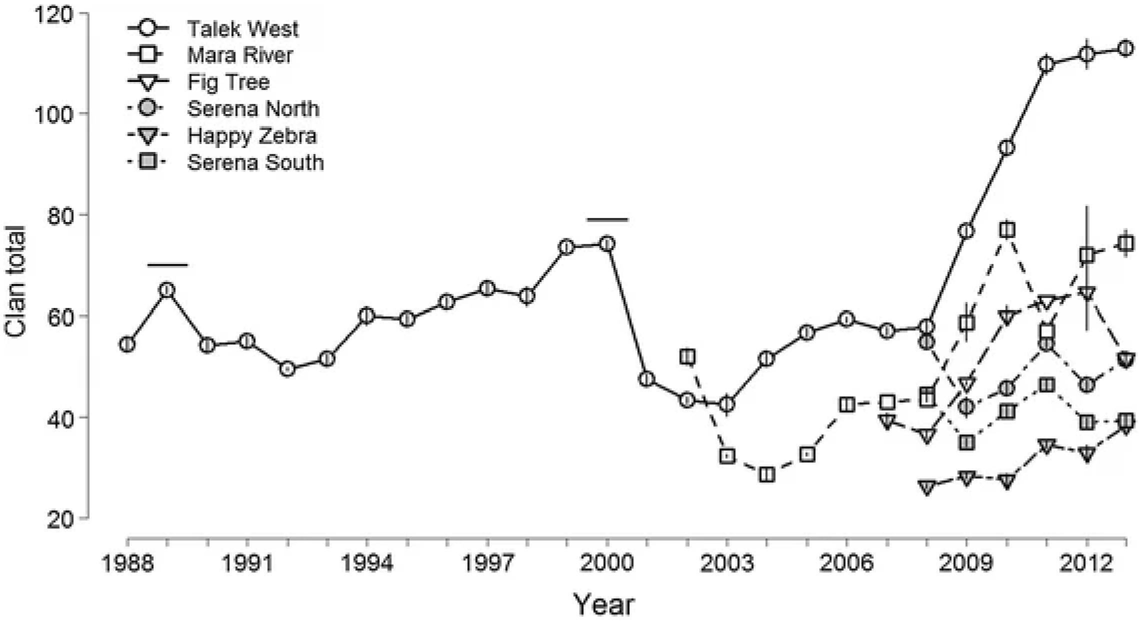
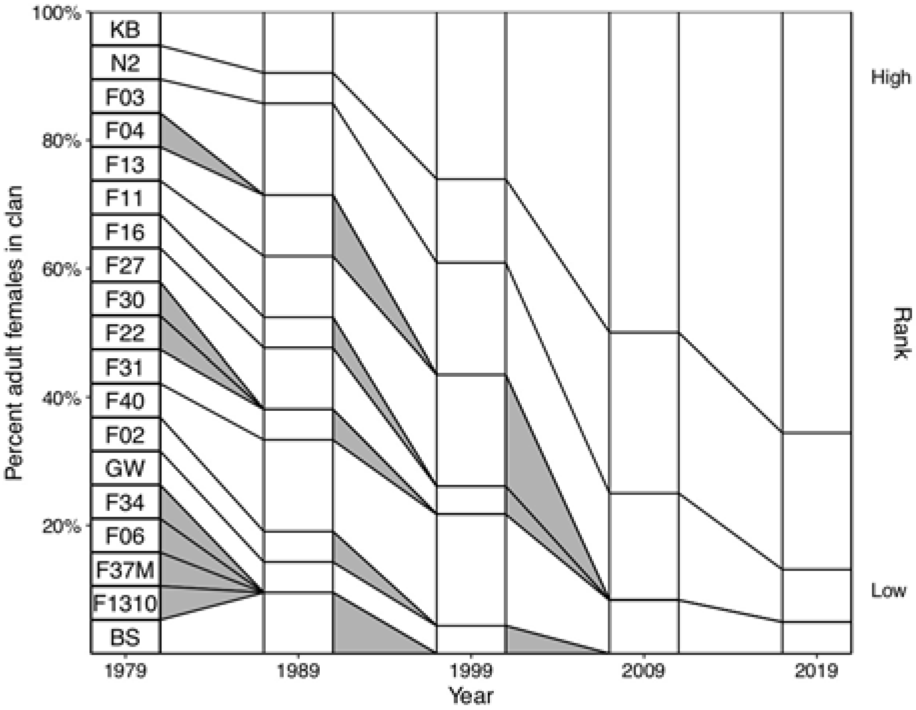


Figure 4.10

Representation among adult female spotted hyenas of the Talek clan at decade-long intervals (Holekamp and Strauss 2020) of descendants of the original 19 adult females studied by Frank (1983). Reproduced from Holekamp and Strauss (2020) with permission from *Integrative and Comparative Biology*.



CHAPTER 5:

SECRETIVE, SCENTED, AND… SOCIAL? FUNCTIONS OF SCENT-MARKING AND NOVEL INSIGHTS INTO COMMUNAL BREEDING IN STRIPED HYENAS

ABSTRACT

Comparative studies of the extant members of the family Hyaenidae have had great utility in illuminating how ecological forces have shaped social evolution in mammals, including hominids. However, the social behavior of one of these species, the striped hyena, remains poorly understood. Striped hyenas were long thought to be strictly solitary, but recent work has suggested that their social behavior is highly plastic and, in some populations, may be similar to that of their closest relative, the brown hyena, in which small groups share a communal den and closely related females cooperatively care for cubs. Here, we investigate striped hyenas' social behavior by conducting the first empirical study of olfactory communication in wild striped hyenas. To test the effects of social and environmental factors on the rate of scent-marking, we extensively radio-tracked six adults females in southern Kenya. Our findings suggest that scent marking in this population functions to advertise individuals' presence to conspecifics. We also describe the first cases of den-sharing and allonursing ever reported in this species. Information regarding striped hyenas' social systems, including hyenas' spatial distribution and care of offspring, should inform the conservation of this threatened species. To better understand the function of scent-marking in striped hyenas, future studies should be conducted on populations in disparate ecological conditions, assess how striped hyenas react to a conspecific's scent mark and examine how these reactions vary based on the sexes of and genetic relatedness between the sender and receiver.

INTRODUCTION

Comparative studies of social ecology in extant species can shed light on the conditions that gave rise to the evolution of group-living in mammalian carnivores. Research on social evolution in carnivores has primarily focused on group-living species, especially those that are diurnal, are large-bodied, and occupy open habitats, as these traits make direct observation more feasible (Clutton-Brock 2016, Smith et al. 2017, Graw et al. 2019, Clutton-Brock 2021). We still know very little about the social behavior of many “solitary” species, which constitute the vast majority of the order Carnivora (Gittleman 1984, Holekamp & Sawdy 2019, Clutton-Brock 2021), especially nocturnal species. Field studies on apparently solitary nocturnal carnivores are critical to advancing our understanding of social evolution in carnivores and, more broadly, in mammals (Clutton-Brock 2021).

Here, we investigate the social behavior of the striped hyena (*Hyaena hyaena*), an elusive nocturnal scavenger. They have been extirpated from much of their historic range and typically persist at low densities in somewhat isolated populations (Holekamp & Kolowski 2009). Striped hyenas have proven difficult to observe in the wild, owing to their low densities, nocturnal and elusive behavior, and wide-ranging movements, as well as the rugged terrain they often occupy. As a result, they are the least studied of the extant hyaenids (Kruuk 1976, Mills & Hofer 1998, Watts & Holekamp 2007, Holekamp & Kolowski 2009, Wagner et al. 2008), and one of the few remaining large carnivore species about which very little is known.

In habitats with abundant resources, striped hyenas’ social organization somewhat resembles that of brown hyenas; they forage solitarily but may convene in small groups of kin at active dens where both subadults and adults may provision cubs with food (Califf et al. 2020). Although social groups of striped hyenas are smaller than those typical of brown hyenas, striped hyenas have been seen aggregating in groups of two to eight, particularly at active dens, where both the fathers and older siblings of den-dependent cubs have been documented participating in their care, including provisioning cubs with food (Bothma & Walker 1999, Wagner 2008, Holekamp & Kolowski 2009, Alam 2011, Jhala 2013, Mandal 2018, Califf et al. 2020, Tichon et al. 2020, Hadad et al. 2023).

One approach to studying the social systems of striped hyenas is to investigate the functions of intraspecific communication in this species (Wooldridge et al. 2019). Social systems, whether they be solitary, highly gregarious, or somewhere in between, are modulated by communication (Bradbury & Vehrencamp 2011, Freeberg et al. 2012, Theis 2008), which serves a myriad of functions, such as promoting social cohesion and avoiding combat between competitors (Yahr 1983, Bradbury & Vehrencamp 2011). Olfactory communication (scent marking) is especially important in maintaining social organization within low-density populations of wide-ranging mammals, including many carnivore species (Garvey et al. 2017, Rafiq et al. 2020). Hyaenids rely heavily on olfactory communication, including defecation and pasting (Smith & Holekamp 2010). Pasting is a form of scent-marking unique to, and ubiquitous among, hyaenids. While pasting, hyenas straddle an object, usually a stalk of grass, and walk forward, dragging it past their extruded anal pouch and depositing a thick, paste-like secretion (Figure 5.1, Figure 5.2, Kruuk 1972, Mills 1989, Theis 2008, Holekamp & Kolowski 2009, Smith & Holekamp 2010). For this reason, the scent secretion of hyenas is called ‘paste.’ A single paste deposition can convey a wide array of information about the sender and may serve multiple intragroup, intergroup, or interspecific functions (Yahr 1983, Theis 2008). Various functions of pasting have been proposed for spotted and brown hyenas, such as to demarcate territories, deter competitors, attract mates, promote social cohesion, or maximize intragroup foraging efficiency (Mills et al. 1980, Theis 2008). Sparse descriptions in the literature suggest that striped hyenas paste frequently while traveling in search of food (Kruuk 1976, Alam 2011), by carcasses (Wagner 2006), and over spotted hyena paste (Kruuk 1976), but rarely near their dens (Kruuk 1976). Striped hyena paste has been presumed to function to demarcate territories, but this has never been tested.

We aim to test three non-mutually exclusive hypotheses about the functions of pasting by striped hyenas (Lewis 2006, Buesching & Jordan 2019) by using direct behavioral observations of radio-collared hyenas and genetic data to identify the social and environmental conditions under which striped hyenas paste at elevated rates. The first hypothesis suggests that the purpose of pasting is self-advertisement (Miaretsoa et al. 2022). Hyenas could maximize the number of potential receivers by pasting in areas used by multiple conspecifics or at resources that attract conspecifics, such as food items. This would only apply to food items that may be subsequently fed on by other hyenas, such as large carcasses, and not to food items small enough to be fully consumed on one occasion, carried to a den, or cached by the focal hyena. Thus, the self-advertisement hypothesis predicts that hyenas' pasting rates should increase with the number of overlapping conspecific home ranges, and hyenas should paste more frequently by large carcasses than by smaller food items.

The second hypothesis suggests that hyenas paste to demarcate territorial boundaries. If intruders are the intended receivers of these signals, one might expect territory holders to paste mainly along the perimeter of their territory, because this maximizes the probability of early detection by an intruder (Gosling 1982, Gorman & Mills 1984, Lewis 2006, Jordan et al. 2010, Rafiq et al. 2020, Miaretsoa et al. 2022). However, if individuals maintain particularly large home ranges, then the length of perimeter per individual may be too large for a border-marking strategy to be economically defensible (Macdonald 1980, Gorman & Mills 1984).

The third hypothesis suggests that pasting functions to demarcate resources. This could serve both to help the focal hyena or its kin to locate a food item in the future, or to advertise itself in places where multiple conspecifics are likely to appear. Under this hypothesis, we predict that hyenas should paste at higher rates in the immediate proximity of large food items or at den sites than elsewhere.

To understand the social structure of the Shompole population of striped hyenas and the role of pasting in maintaining this structure, we recorded hyenas' behavior through direct observations and camera trapping. We statistically test ecological predictors of the rate of pasting and briefly describe encounters between individuals and groundbreaking observations of biparental care, communal breeding, and alloparenting, including the first observed case of allonursing ever reported in striped hyenas.

METHODS

Study area

We collected data for twenty-four consecutive months (February 2007-February 2009) on the Olkiramatian and Shompole Maasai group ranches (~ 1,000 km^2). This study area abuts the Shompole Conservancy on its southwest border. This semi-arid region received 317.5 ± 63.5 mm of rainfall annually and had temperatures of 24.2 (mean low) to 37.7° C (mean high). The study area is flat, with an altitude of 900 m above sea level, but bounded by escarpments, lava ridges, and valleys. The sandy, relatively open terrain is covered by *Acacia* woodlands and grasslands, alkaline grassland flats, riverine forests, swamps, and salt pans. The Ewaso River serves as a critical water source for people, livestock, and wildlife. In the dry season, small waterholes allow life to persist away from the river. These waterholes are sparse and dispersed at great distances. For approximately six months out of each year (during the dry seasons), the local Maasai pastoralists occupy the study area and graze their livestock there (mean monthly density: 59.1 ± 17.0 shoats/km^2 and 15.8 ± 5.7 cattle/km^2, Schuette 2012, Schuette et al., 2013). The communities of native ungulates and carnivores are largely intact (Schuette et al. 2013). Herbivores occur at high density (mean monthly density of zebra, Grant's gazelle, wildebeest, impala, and giraffes: 28.16 ± 9.24 individuals/km^2, Schuette 2012), and 20 carnivore species occupy this area, including spotted hyenas and lions (Schuette et al. 2013).

Capture and collaring

We identified 40 individual striped hyenas based on their unique stripe patterns (Spagnuolo et al. 2022). Of these, we captured 20 hyenas (f=11, m=9) in soft-catch foot-hold traps and anesthetized them by injecting a sedative (either 6.5 mg Telazol/kg body weight or a combination of 3.6 mg Ketamine HCl/kg and 0.06 mg Medetomidine HCl/kg) in a plastic dart delivered via a CO_2-powered rifle. Once anesthetized, we determined the hyena's sex and collected blood and tissue samples for genetic analysis. Of the 20 captured hyenas, twelve subadults and adults were fitted with collars. Nine (f=6, m=3) were fitted with VHF collars (Telonics, Inc., Mesa, AZ, U.S.A., or SirTrack Ltd., Havelock North, NZ), and three (f=1, m=2) were fitted with GPS collars (Savannah Tracking Ltd, Nairobi, Kenya). Geographic fixes from GPS collars were downloaded automatically every 20 minutes. All sampling procedures were approved by the Institutional Animal Care and Use Committee at Michigan State University (AUF 07/08-099-00) and met guidelines approved by the American Society of Mammologists (Sikes et al. 2011).

Behavioral sampling

We conducted concurrent focal follows of individual hyenas (Altmann 1974) from a vehicle every night to collect behavioral data. To collect data during the stiped hyena's nocturnal period of peak activity, we conducted observations between 1830 and 0630 hours. We located subjects opportunistically or through radio telemetry and followed them all night or as long as the terrain and other conditions allowed. Subjects were followed at minimum distances of 100 meters for spotlight-habituated hyenas and 200 meters for non-habituated hyenas. During focal follows, we conducted scans every ten minutes and included the subject's GPS coordinates, the behavior(s) in which it was engaged, and the social and environmental contexts. Additionally, we recorded all occurrences of critical incidents, which included feeding, caching food, and pasting.

Camera trapping

We placed two motion sensitive trail cameras with infrared flashes (Moultrie Game Spy digital camera, 6.0 megapixel) at each active den site. We programmed one camera to capture three still images at 15 second intervals when triggered. We programmed the second camera to capture a five-second video followed by a still image. After downloading the resultant photos and videos, hyenas visible in each image were identified by their unique stripe patterns (Spagnuolo et al. 2022).

Analyses of genetic relatedness

We extracted DNA from blood and tissue samples. We used ten microsatellite markers previously developed to investigate paternity in spotted hyenas (Wilhelm et al. 2003) to genotype striped hyenas (methods described in more detail in Libants et al. 2000, Wilhelm et al. 2003, Wagner et al. 2007). One locus was monomorphic, and therefore uninformative, so we omitted it from our analyses. Based on the remaining nine loci, we compared the genotypes of offspring to those of candidate parents within the Shompole population to assign parentage using Cervus 3.0 software.

For each candidate parent, there exist two alternative hypotheses: either (H1) the candidate parent is the true parent, or (H2) it is not. We divided the likelihood of H1 by the likelihood of H2 to calculate likelihood-odds ratio for each candidate, and then calculated the natural logarithm of the likelihood-odds ratio (LOD score). An LOD score greater than zero indicates that the candidate parent is more likely to be the true parent than a conspecific chosen at random from the population (Kalinowski et al. 2007).

The most likely parent is the candidate assigned the highest LOD score. The statistical confidence (Δ) equals the difference between the LOD score of the most likely parent and that of the second most likely parent (Kalinowski et al. 2007). Parentage was only assigned if a candidate had an LOD score greater than zero and a Δ value greater than 80% of the LOD score. Comparing genotypes at multiple loci increases the probability of genotyping errors, which may lead to false exclusion of a true parent. Cervus implements corrected likelihood equations (Kalinowski et al. 2007) to accommodate possible genotyping errors when calculating the LOD score for each candidate parent.

Spatial and statistical analyses

We empirically tested our predictions using behavioral data from hyenas of known sex that were observed for a minimum of 24 hours each. All spatial and statistical analyses were performed in R Statistical Software version 4.2.3 (R Core Team 2023) and RStudio version 2023.09.0 (Posit Team 2023). All generalized linear mixed models were performed using the ‘glmmadmb’ function in the ‘glmmADMB’ R package (Fournier et al. 2012, Skaug et al. 2016).

Subjects’ locations were recorded via GPS collars and direct observations. We estimated the home range of each adult hyena for which a minimum of 50 locations were recorded. Because the location data were highly autocorrelated, we estimated individuals’ 95% Autocorrelated-Gaussian reference function Kernel Density Estimation (AKDE, Noonan et al. 2019) home ranges using the ‘akde’ function in the ‘ctmm’ R package (Calabrese et al. 2016, Fleming & Calabrese 2023).

We tested the self-advertisement hypothesis and the territory demarcation hypothesis by analyzing spatial predictors of pasting. We applied a 400 x 400 m resolution fishnet grid to our study area. For each focal hyena, we extracted the following data for each grid cell: the total number of conspecifics’ home range intersecting the cell (excluding that of the focal hyena), the distance from the cell centroid to the nearest boundary of the focal hyena’s home range, the total number of pastes observed, and the total duration of observer effort (each ten minutes of observer effort was represented by one point). Thus, each cell ID-hyena ID pair represented one datum. We excluded data for which less than 30 minutes of observer were allocated. We fitted a zero-inflated negative binomial generalized linear mixed model of paste count with main effects of the number of overlapping conspecific home ranges and the proximity to the focal home range boundary, an offset for observer effort, and a random effect of subject ID.

To test the resource demarcation hypothesis, we compared pasting rates among behavioral contexts: at a den, by a large carcass (>60 kg) or “small” food item (<60 kg), and traveling (not carrying food). The den context includes any time spent at an active den (whether food was present or not), the food category refers to any period of time during which the focal hyena was in the presence of a food item away from an active den, and the traveling category includes observations during which the focal hyena walked rapidly for a long distance. We excluded observations during which the subject was resting.

We divided each observation session into sub-sessions during which a hyena was engaged in each specific behavioral context; whenever the behavioral context changed, we considered it to be the beginning of a new sub-session. Each sub-session represented one datum, for which we extracted the subject ID, duration of the sub-session, and the number of times the subject pasted during the sub-session. We fitted the pasting count as a function of behavioral context with an offset for observer effort (sub-session duration) and a random effect of subject ID, using a zero-inflated generalized linear mixed model with a negative binomial distribution.

RESULTS

Sample sizes

Over the course of the study, we identified 27 adults (f=9, m=5, u=13), three subadults (f=1, m=2), and ten cubs (f=1, m=2, u=7). We conducted 922.6 hours of direct observations and observed 643 pasting events performed by 22 different hyenas (Figure 5.1). Eight of these hyenas met the criterion for inclusion of behavioral data in our analyses (a minimum of 24 hours of direct observations; six adult females, one adult male, and one male cub), yielding 727.2 hours of direct observations and 628 observed pastes, of which 586 pastes had associated geographic coordinates recorded. Geographic fixes for the GPS-collared hyenas were collected for 26 days from the female and for 21 and 169 days from the two males, respectively. Without VHF collars, these hyenas were rarely located for direct observations. Therefore, we included their home range estimates in the relevant analyses, but not their behavioral data.

Home ranges

Based on locations recorded during direct observations, the 95% AKDE home ranges of the female subjects had a mean (± standard error) area of 41.75 ± 3.13 km^2 (n=6), while the males' home ranges had a mean of 27.68 ± 12.07 km^2 (n=2). Additionally, estimated home range areas of the hyenas bearing GPS collars were 49.72 km^2 for the single female and 66.11 ± 3.37 km^2 for the two males. Overall, the mean home range area sizes for females (42.88 ± 2.88 km^2, n=7) and males (52.73 ± 7.29 km^2, n=4) did not differ significantly (t = -1.14, df = 3.77, p = 0.32). Due to limited accessibility, we could not conduct observations in the large, wooded area surrounding a swamp. Therefore, if this was part of any of the subjects' true home ranges, it would not be reflected in our home range estimates. Eight home ranges converged on a long strip of woodland, which may seasonally become inundated with water.

Foraging Behavior

In 114 observations of feeding, hyenas primarily fed on native ungulates (n=70) and livestock (n=22). We observed them feeding on a carcass 58 times, a small scrap 40 times, and a small rodent or insect 10 times, and observed 6 successful hunts (three Grant's gazelle calves, one shoat, one flamingo, and one civet). Additionally, we observed 31 test chases or attempted kills (17 rodents/insects, 20 native ungulates, two birds, one hare). Of the native ungulate feeding events, 24% were zebra, 20% were Grant's gazelle, 17% were wildebeest, and 16% were impala. Hyenas most frequently pursued Grant's gazelle calves, and successfully killed the calf 23% of the time (three out of 13). Young hyenas sometimes test chased prey that were clearly too large for them, including a giraffe. Two hyenas were seen feeding on the same carcass at approximately the same time on two occasions (an unrelated adult male-female pair, F110 and M114, and the adult mother-daughter pair, F104 and F105). Once, we observed two hyenas visit the same carcass at different times; F110 investigated a one-day-old goat carcass, and two hours later, F104 was seen feeding on this carcass. F104 was seen inside unoccupied shoat pens on multiple occasions and killed and ate a shoat on one occasion. This was the only incident of livestock depredation observed over the course of this study.

We observed hyenas cache food on ten occasions, and only once did a hyena paste at the cache site. Once, a female retrieved a cached scrap, immediately cached it again, and retrieved it again two hours later. Hyenas typically fed from a carcass before tearing off pieces to cache, but once, a female killed a flamingo and cached it without eating any of it first.

Partial pedigree

A partial pedigree was constructed based on direct behavioral observations (e.g., lactating mothers with dependent cubs) and parentage assigned through Cervus 3.0 (mothers and fathers, Figure 5.3). In only one of three litters of twins were the cubs full siblings, reflecting analytical limitations or, more likely, multiple paternity.

Denning, den attendance, and parental care

During the study period, we observed eight litters of den-dependent cubs borne by five different mothers (F101, F104, F105, F110, and F116). We observed one to three litters per mother during the study period, and one to three cubs per litter. We located a total of 37 den sites, each of which was a burrow in the earth, rather than a rock structure, and was located immediately next to a large bush. Dens occurred in mixed habitats of open (barren dirt or grass) and closed habitat (bush or scrub). Dens were used for an average of 12.67 continuous days after we discovered them. F110 used 14 different den sites. An adult mother-daughter pair (F105, mother; F104, daughter) used seven and 21 different den sites, respectively, and six of these sites were used by both females at some point during the study (not necessarily concurrently). F104 never used a den outside of her mother's home range. On two occasions, F104 and F105 shared a single den concurrently for their two respective litters (previously reported by Califf et al. 2020). At both shared dens, F105 began using the den first, her adult daughter F104 joined her (for 13 and 65 days, respectively), and both abandoned the den on the same date.

We directly observed hyenas at dens on 123 unique dates. Dens in use by F101 were observed on 31 unique dates; dens in use by F104 and/or F105 were observed 74 different times, and dens in use by F110 were observed 17 different times. Hyenas that were seen together at an active den two or more times over the course of the study, most often members of an extended family, are henceforth considered to be "familiar" with one another. Adult male M103 was observed at the den in use by F101 and her cubs F108 and M109 (both were M103's offspring) on eight different occasions.

Adult females F104 and F105 were seen together or with each other's offspring on 13 different occasions at six different den sites. On several occasions, one of these adult females stayed with the other's cubs during her absence. F104 groomed Junior on one occasion, and, unexpectedly, F105 was seen nursing one of F104's cubs (M113). These females were not observed provisioning each other's cubs with food while sharing a den, but eight months later, F104 provisioned F105's newest cub (Feo) with food. Once M113 was over one year old, he was seen at his mother's den site with Feo, his aunt (although younger than he was), on four occasions, during which he played with Feo and provisioned her with food.

Our camera traps revealed a long-term association between M113, F117, and F110. M113 began frequently visiting F117 at the den when she was still den-dependent, but around the time when her mother (F110) gave birth to a new litter. F117 spent a great deal of time with her three younger siblings at her mother's (F110's) next den and was seen grooming her younger sibling while their mother (F110) was away from the den (Figure 5.4), and grooming F110's face while F110 nursed her own den-dependent cubs (Figure 5.5). F117 was once detected nursing from her mother before the younger cubs took over nursing. M113 associated with F110 and F117 at four different dens over the course of over four months and he was allowed in immediate proximity of the den hole and F110's small, vulnerable cubs. M113 and F110 frequently played or rested together, and occasionally groomed one another. M113 mounted F117 several times on one occasion, although it is unknown whether copulation took place or if this was play (Figure 5.6).

Encounters away from dens

In 48 observations of two or more hyenas together away from a den, only two were antagonistic; F101 chased away an unidentified adult, and F110 chased away F104. In both cases, the chased hyena fled the area. No physical contact was observed. One unrelated pair of adult females (F105 and F110) were seen together once without any aggression. We saw an adult female (F101) with the father of her youngest litter (M103, who attended the den frequently) on five occasions, a mother traveling or resting with her youngest cub(s) 16 times, a mother with a female cub from her previous litter four times, the adult daughter-mother pair (F104 and F105) ten times, and two subadult littermates without their mother present once. F105 traveled with her grandcubs twice when F104 was not present, once following them as they left their den.

We found unrelated hyenas F110 and M114 together three times within three months. Once, they fed on a carcass together without any aggression. Another night, they traveled together, occasionally stopping to rest. M114 occasionally sniffed F110's anus. Four and a half months after their last known encounter, F110 was seen with a new litter, but we do not have an approximate date of birth for those cubs. The only other sighting of an unrelated male-female dyad without known cubs was F105 and M103.

Hypothesis testing: Pasting for self-advertisement and territorial demarcation

We modeled paste count as a function of the number of conspecifics' home ranges overlapping a given location and proximity to the focal hyena's home range boundary. This analysis was based on 634 hours of direct observations and 586 observed pastes across eight subjects (Figure 5.7). The total observation effort per each observed number of conspecifics' home ranges (excluding that of the focal animal; zero to eight) at a given site ranged from 8 to 198 hours, with the highest effort expended where three or four conspecifics' home ranges converged (118 and 198 hours, respectively). The pasting rate significantly increased by 0.29 ±0.07 (estimate ± std. dev.) with the addition of each overlapping conspecific home range ($p < 0.0001$, Figure 5.8). Proximity to the boundary of the focal hyena's home range had no predictive power over the observed rate of pasting (-0.0002 ± 0.0002, $p = 0.42$).

Hypothesis testing: Pasting to demarcate resources

The analysis of paste count as a function of behavioral context was based on 535 hours of direct observations and 613 observed pastes ($n_{\text{sub-sessions}} = 3{,}283$). During our nightly observations, subjects spent 55% of their overall time traveling. Subjects pasted at estimated rates of 0.025 pastes per hour (0.0023-0.26, 95% confidence intervals) at active dens, 5.81 pastes per hour by large food items away from dens (1.15-29.34), 1.16 pastes per hour at small-to-medium food items away from dens (0.42-3.23), and 2.52 pastes per hour when travelling (0.70-9.02). The pasting rate by large food items was significantly higher than that at small food items ($p = 0.011$) or active den sites ($p < 0.0001$) but was not significantly higher than the rate when travelling, ($p = 0.121$, Figure 5.9). The pasting rate was significantly higher when travelling than when at a den site ($p < 0.0001$) or at a small food item ($p < 0.05$). Hyenas pasted more frequently at small food items than at dens ($p < 0.0001$).

DISCUSSION

Hyenas in this population not only exhibited social tolerance of kin but appeared to engage in cooperative care of offspring by male and female older siblings, fathers, and, in one case, a grandmother. An adult mother-daughter pair displayed the first-ever reported cases of den-sharing in this species, and the mother in this pair provisioned her grandcubs with carrion and, on one occasion, even nursed a grandcub, which has never before been reported in striped hyenas. Siblings from previous litters have been known to serve as helpers for raising their den-dependent siblings in several populations (Alam 2011, Califf et al. 2020, Hadad et al. 2023, Mandal 2018). Scavenging is a time-consuming foraging strategy that limits the frequency with which a mother can attend her den and bring food to her cubs. This foraging strategy may select for cooperative care of offspring, because making fewer stops at the den should allow mother hyenas to forage more efficiently. The feeding ecology of striped hyenas and their closest relative, brown hyenas, are strikingly similar (Holekamp & Kolowski 2009). In brown hyenas, clanmates share a communal den, both males and females provision offspring, and females nurse cubs other than their own (Owens and Owens 1979, 1984, Watts & Holekamp 2007).

We tested three potential functions of pasting in this population: self-advertisement, territory demarcation, and resource demarcation. Territorial demarcation has been presumed to be the primary function of pasting in striped hyenas, but this is the first study to empirically test this. We found no evidence to support the role of territorial demarcation in pasting within this population. Home ranges between mixed-sex dyads and female overlapped substantially (Califf et al. 2020), but the mechanisms by which hyenas prevent encroachment by unrelated competitors are unknown. We only observed two confirmed encounters between unrelated adult females. One of these encounters was peaceful, whereas the other resulted in an aggressive physical confrontation. A similar confrontation was observed in another pair of hyenas, but the identity of the recipient of aggression could not be determined.

We found strong support for the hypothesis that pasting plays a role in self-advertisement. Hyenas exhibited the highest rates of pasting when near large carcasses, when traveling, and where the home ranges of many hyenas intersected. These home range junctions may be thought of as “information centers” (Wolff et al. 2002) that are so important for gathering information or advertising oneself that it is worth traveling far outside of one’s home range to access these hubs. These junctions occurred along a stretch of dry creek bed, a potential seasonal water source that is lined by riparian vegetative cover. Rainfall in this region is seasonal and highly variable across years, and the only permanent fresh water source is the Ewaso Nyiro River (Downing 2005, Schuette 2012, Connolly et al. 2021). As a result, water sources are temporally and spatially heterogeneous and represent a limiting resource. Furthermore, dense riparian vegetation provides critical habitat for striped hyena dens and daytime refugia for adults to rest at safely (Schuette 2012), as well as providing shelter from the heat of the sun (Jhala 2013). Future work on striped hyenas in this region should record the locations of water sources throughout the year and incorporate these data into spatial analyses, as these likely serve as particularly important hubs for gathering information and for self-advertisement via pasting.

The elevated rate of pasting observed in immediate proximity to large carcasses could be explained by either the self-advertisement hypothesis or the resource demarcation hypothesis. The reactions of hyenas to these scent marks, and how the relationship between the sender and receiver modulates these reactions, would better parse out these mechanisms. Our observations of encounters away from den sites were too sparse for us to address this, but we observed groups of two to three hyenas sharing a carcass, two unfamiliar hyenas feeding from the same carcass on different occasions, and an individual feeding from the same carcass on two different occasions. This suggests that pasting at carcasses may be an effective method of self-advertisement. Hyenas have been reported sharing a carcass in other populations as well (Jhala 2013).

Consistent with studies of other populations (Kruuk 1976, Bothma & Walker 1999), we rarely saw hyenas paste at dens. This contradicts predictions from both the resource demarcation and self-advertisement hypotheses. Pasting must not be necessary to signal ownership of a den once the cubs have been born, since this information would be redundant with the cubs' presence. However, active dens should be useful for self-advertisement via pasting; dens were frequently visited by familiar hyenas while cubs resided in them, and therefore could be effective places to deposit paste as well as to signal continued group membership through pasting (Theis 2008, Burgener et al. 2009, East et al. 2013) or anoint oneself with the signature group scent through overmarking (East et al. 2013). Indeed, striped hyenas have been known to defecate in latrines near communal dens (Jhala 2013). The communal den also serves as a group's social center in brown and spotted hyenas, and group members frequently paste there (Hofer & East 1993, Bothma & Walker 1999, Theis 2008). Perhaps the benefits of pasting at dens are outweighed by the costs for striped hyenas; in our study population, predators were frequently seen near, or even in, the dens. The presence of dominant predators has been known to inhibit scent-marking in other carnivores, thus interfering with intraspecific self-advertisement (Cornhill & Kerley 2020), although the reason for striped and spotted hyenas' tendency to overmark each other's paste (Kruuk 1976) remains a mystery.

This study further elucidates the social system of the Shompole striped hyena population and, thus, the behavioral differences among populations across ecological gradients (Wagner 2006, Wagner et al. 2007, 2008, Califf et al. 2020). Collectively, the behavior exhibited by these populations, as well as others across their global range (Tichon et al. 2020, Hadad et al. 2023), demonstrates the considerable plasticity in social behavior of this species. A more accurate and thorough understanding of the behavioral ecology of striped hyenas, especially as it relates to social behavior, holds great value for advancing basic research on social evolution in mammals and has implications for the conservation of this rare but ecologically important species. The behavioral and ecological diversity observed within Hyaenidae (Holekamp & Kolowski 2009, Holekamp & Sawdy 2019) makes this family an exceptional model taxon in which to study how ecological pressures have driven the evolution of various social systems throughout carnivores as well as other mammals (Smith et a. 2012). Understanding ecological predictors of social grouping in striped hyenas could also aid their conservation by facilitating more accurate estimation of density across ecological gradients, leading to more accurate global and local conservation statuses and more informed local and regional management (Akçakaya et al. 2006). This would also help us to predict how their populations may respond to habitat fragmentation and loss, human activity, and climate change (Singh 2008, Gall et al. 2022). Striped hyena conservation is particularly important because, as scavengers, they play important roles in ecosystem structuring, stability, and resilience (Wilson & Wolkovich 2011, Beasley et al. 2015).

FIGURES

Figure 5.1

Female F117 pastes on a stalk of grass.

Figure 5.2

Striped hyenas, like spotted hyenas and aardwolves, deposit a long-lasting white secretion when pasting. Shown here is striped hyena paste that has been deposited onto a stalk of grass.

Figure 5.3

This pedigree includes all identified hyenas. Pink boxes represent females, blue boxes represent males, and black boxes represent hyenas of unknown sex. Confirmed littermates are denoted by a dotted-black line. Black arrows indicate parentage. If the most likely father could not be identified for a given hyena, only its mother is indicated. Cervus 3.0 identified M109 was the most likely father of M113, but M109 was not yet reproductively mature when M113 was conceived. They likely share a recent male ancestor, but not the same father.

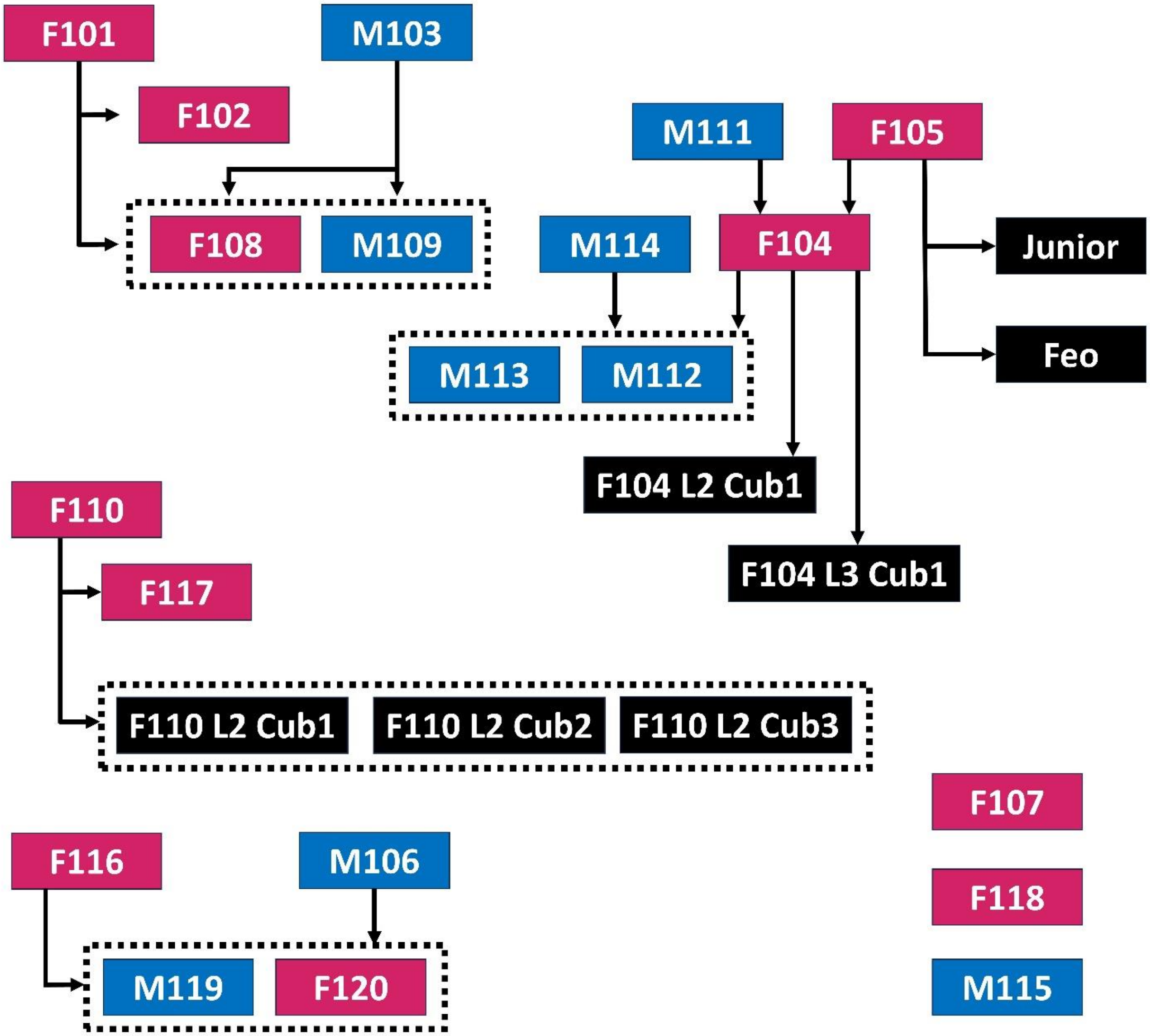


Figure 5.4

F117 remains at her mother's den with her three young, vulnerable siblings while her mother is away, presumably foraging. Here, she grooms one of her younger siblings' anogenital region.

Figure 5.5

F110 (right) lies down to nurse her three youngest cubs. Meanwhile, her daughter from a her most recent previous litter, F117 (left), stands and grooms F110’s face.

Figure 5.6

(a) M113 (right) and F117 (left) frequently played, as shown in this image, where both are displaying open mouth face, a ritualized signal in social play of spotted hyenas (Nolfo et al. 2022). They also romped around the den, chasing one another. (b) F117 (front, left) and M113 (back, right) rest together at F110’s den while the three young cubs are out of sight, likely inside the den. (c) F117 (left) and M113 (middle) play while F110 (right) stands looking into the distance. (d) M113 reaches over F117’s hips with his left foreleg and gently pulls her towards him, so that he can straddle her in a mounting position.

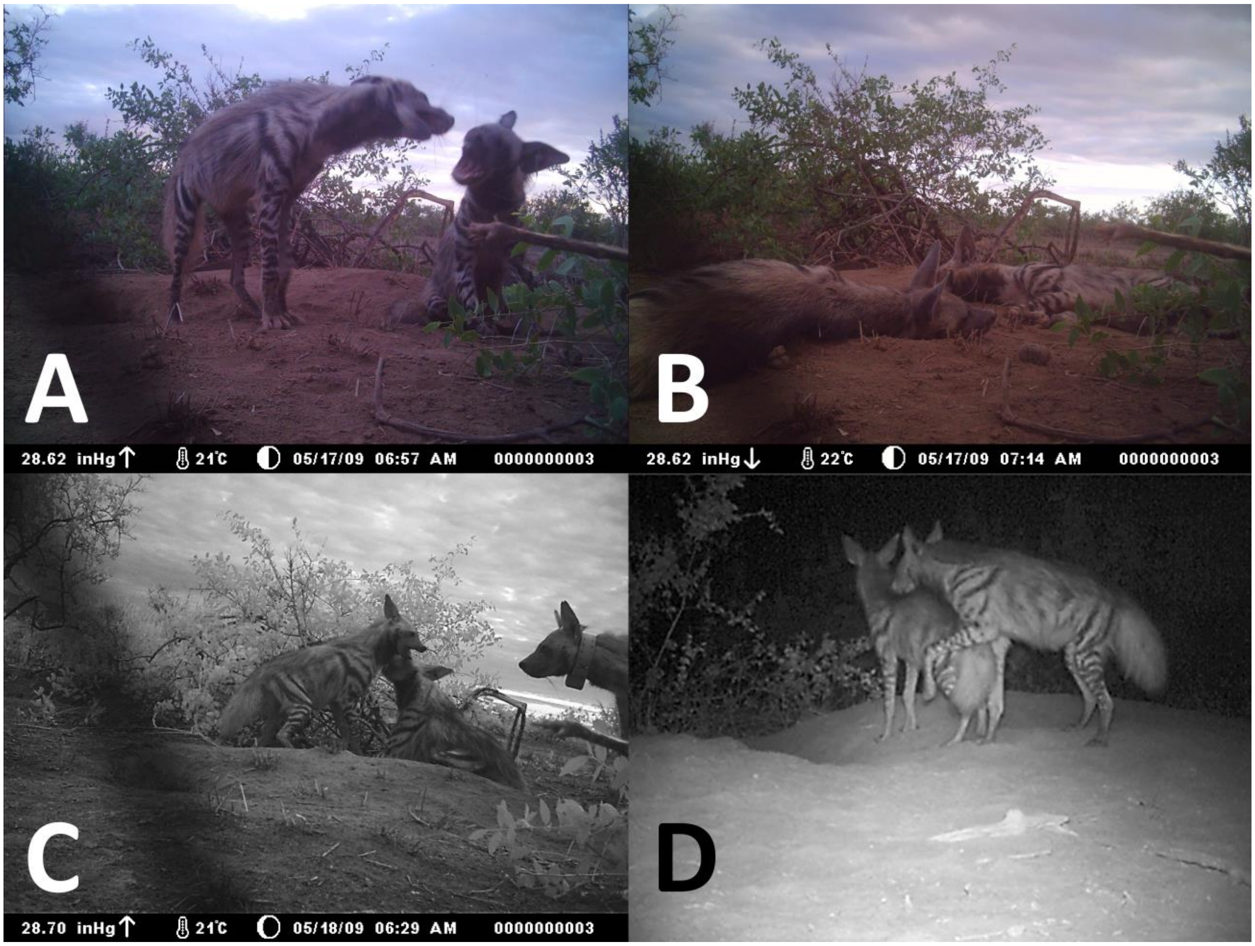


Figure 5.7

95% AKDE home range estimates are represented by semitransparent polygons (focal females, pink; focal males, blue; GPS-collard hyenas, gray). Observed pastes (black) occurred at the highest density in two clusters, each of which corresponds with the grassland habitat where the highest number of hyena home ranges overlap.

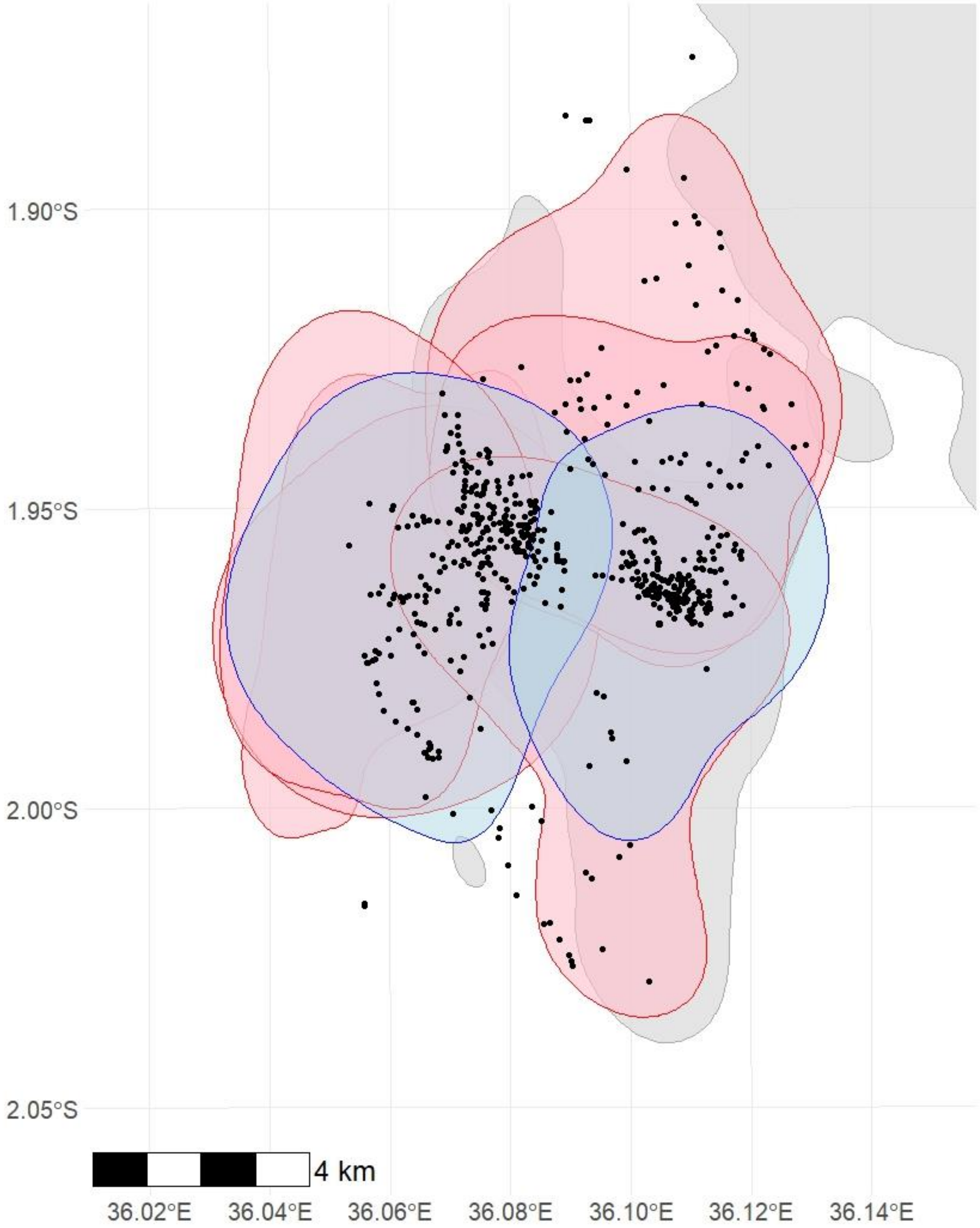


Figure 5.8

The solid line and shaded region represent the pasting rate per hour and standard error, as predicted by the model, at each number of overlapping home ranges.

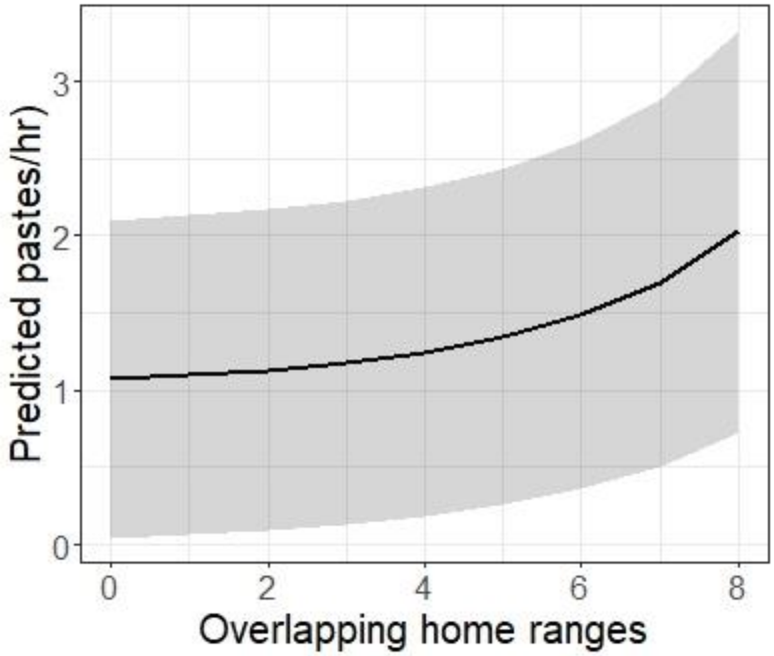
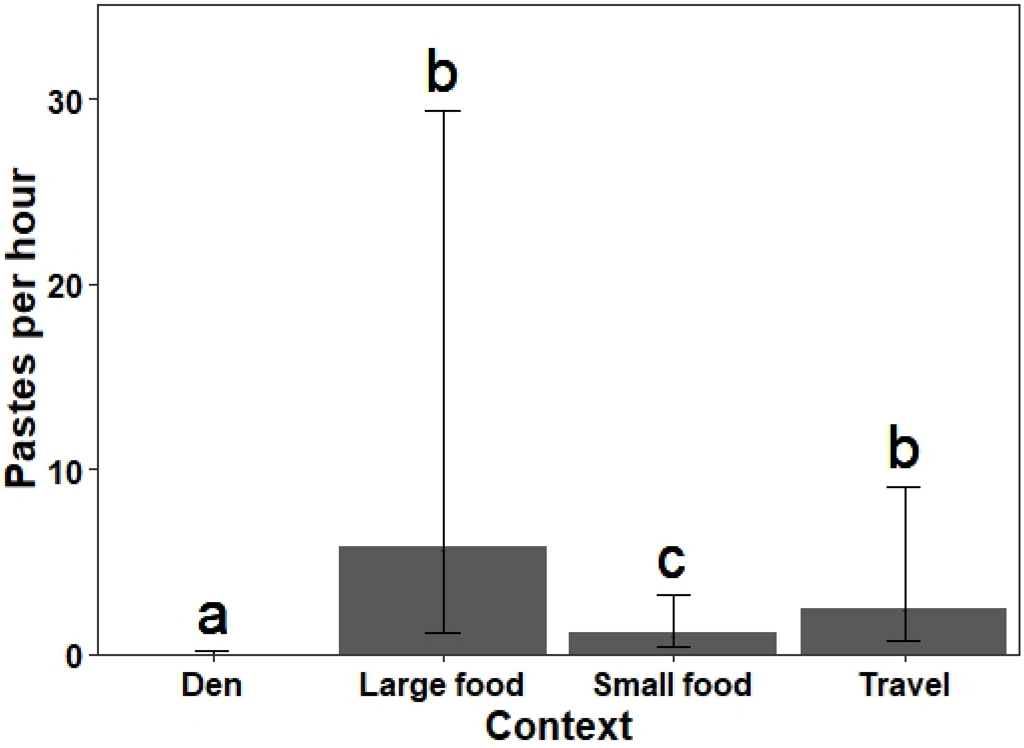


Figure 5.9

Boxes indicate the estimated paste rate in each behavioral context, whiskers indicate the 95% confidence intervals for each estimate, and letters indicate statistical significance. The pasting rates were highest in the context of large food and travelling, and lowest at den sites.



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