Baboon Anti-Predator Strategies in the Soutpansberg Mountains, South Africa

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Primate and Predator Project Camera Trap Grid

Abstract

Predator movement through an ecosystem is an important driver of prey behavior. In South Africa's Soutpansberg Mountains, the relationship between leopards and chacma baboons represents a key predator-prey dynamic. This study focused on the influence of leopard activity on chacma baboon anti-predator behavior by addressing two questions: (1) *To what extent might leopard activity correlate with baboon movement?* and (2) *Do baboons behave differently in high-risk and low-risk areas?* I predicted that leopard movement would influence baboon movement and behavior more in areas of high predation risk, with baboons exhibiting smaller group spread and moving more quickly during these times as well as displaying higher vigilance rates and lower rates of social and foraging behaviors. To address these hypotheses, I used GIS to interpret GPS collar data by defining the habitats falling within each species' home range. I also collected scan data on baboons to examine the influence of leopard activity on baboon behavior. Baboons preferred rocky habitats and leopards forested ones. Proximity events occurred significantly more often than expected in bush habitats and significantly less often than expected in open habitats. In addition, baboon activity significantly increased following a proximity event, but group spread did not change. Baboons scanned significantly more than expected in grassland, rocky, road, farm, and high-use leopard habitats and significantly less than expected in forest, bush, and low-use leopard habitats. Lastly, baboons foraged significantly less than expected and exhibited significantly more social behaviors than expected in high-use leopard areas. The results of this study could help to focus conservation efforts in the area by shedding light on the spatial ecology of leopards and baboons, indicating which areas they use most intensely and thus should be protected. This study is particularly important considering that the IUCN is expected to change leopards' conservation status from "Near Threatened" to "Vulnerable" in 2016.

Table of Contents

Figures

Tables

Introduction

Understanding how animals use their environments and the factors that influence their use of space is key to studying their ecology (Willems and Hill 2009; Hill 2006; Bailey 1993; Burt 1943). One such factor is predator activity. Predation is an important driver of animal evolution and the predator-prey relationship is a ubiquitous one (*e.g.* Klailova 2013; McGraw and Berger 2013; Bidner 2009; Huffaker 1958; Gause *et al.* 1936). As noted by Day *et al.* (2002), predation is a fundamental element of species' interactions, vital in both balancing complex ecosystems and exerting selection pressure. Prey species may alter their movement and behavior in response to such predation pressure in a variety of ways – by adjusting their ranging behavior, habitat preference and refuge use, group size and spread, and alarm call and vigilance rates (Cowlishaw 1996; Lima & Dill 1990; Burt 1943). These activities change based upon prey estimates of predation risk within a particular ecosystem or at a particular time (Lima 1998a; Abrams 1994; Lima and Dill 1990).

There are many environmental factors that influence anti-predator behavior (Bidner 2009). For example, prey species may adjust their levels of anti-predator behavior depending upon habitat type and how close they are to refugia, as both of these factors influence how easily a predator is able to detect and capture prey (van der Meer *et al.* 2012; Bidner 2009). It is widely accepted, however, that primates may sometimes have an imperfect perception of their own predation risk (Mourthé and Bernett 2014; Bidner 2009). Accordingly, animals often exhibit anti-predator behavior in a manner inconsistent with the degree of threat they actually face. For example, Hill and Coleman (2014) found vervet (*Chlorocebus pygerythrus*) and samango monkeys (*Cercopithecus albogularis*) living within the same area, and thus exposed to identical predator guilds, to exhibit anti-predator behavior at different levels of intensity.

One significant predator-prey relationship exists between primates and large carnivores. Predation risk is a major influence on primate ecology and evolution, as most primates face the threat of predation in their natural habitat (Hart 2000). Many studies have found that predation pressure influences which habitat type primates frequent (Bidner 2014; De-Raad 2012; Hill and Cowlishaw 2002, Cowlishaw 1994, Burt 1943). For instance, Matsuda *et al.* (2010) uncovered predation threat from Malaysian clouded leopards (*Neofelis nebulosa*) as the driving force behind proboscis monkeys' (*Nasalis larvatus*) proclivity for riverine habitats (Matsuda *et al.* 2010). Furthermore, habitat visibility can be an important element of risk reduction (Cowlishaw 1997). How dense or open a habitat is can influence the probability of encounter, attack, and successful prey capture, as hunting success increases with greater cover for ambush predators such as leopards, tigers, and cougars (Balme *et al.* 2007; Husseman *et al.* 2003; Karanth and Sunquist 2000). This phenomenon is in accordance with Balme *et al.* (2007) and Hopcraft *et al.* (2005) who found that large African carnivores such as lions and leopards (*Panthera pardus*) prefer to hunt in areas where prey is easily taken rather than where prey is most abundant. This relationship between hunting success and habitat density likely influences primates' tendency to preferentially feed in good-visibility habitats 'safe' from leopard predation, even when riskier areas are more food abundant (Cowlishaw 1996).

Another important predation-related behavior in primates is group spread. A study on chacma baboons (*Papio ursinus*) found their group spread to be lower in high-risk areas, allowing them to more easily mob approaching predators (Bidner 2007). This behavior is not unique to chacma baboons. Studies have found a range of primates, for example tamarins (Smith *et al.* 2005) and wooly monkeys (Schmitt and Di Fiore 2015), to constrict group spread in response to predation threat.

Primates also display a variety of behaviors that allow them to detect predator presence, such as increasing vigilance in areas of high predation risk (Cowlishaw 1996). A study in Tsaobis Leopard Park in Namibia found that chacma baboons spent a greater proportion of their time vigilant when far away from refugia. Other researchers have found colobus monkeys (*Colobus vellerosus*) and baboons to increase their vigilance in denser habitats and in areas that are intensively used by predators (Teichroeb and Sicotte 2011; Hill and Cowlishaw 2002; Cowlishaw 1998; Cowlishaw 1996; Devore and Washburn 1963).

Studies have also documented predation risk as influencing primates' activity budgets, with primates being less likely to engage in social and foraging behaviors in high-risk habitats (Cowlishaw 1996; Cords 1995). In her study on blue monkeys (*Cercopithecus mitis*) in Kenya, Cords (1995) suggested that affiliative behavior such as grooming is costly because they reduce the amount of time primates spend scanning for predators and thus reduce the monkeys' ability to avoid attack. She proposed that these monkeys preferentially groomed at low-risk times and places. Cowlishaw (1997) supported these results, finding chacma baboons to exhibit tradeoffs between anti-predator behavior and both grooming and foraging. These anti-predator strategies seem to be in response to perceived predation risk, or a primate's estimation of the likelihood it will be attacked by a predator, rather than a reflection of actual predator presence (Hill and Weingrill 2007).

The relationship between chacma baboons and leopards involves these kinds of anti-predator behaviors (Jooste *et al.* 2013; Cowlishaw 1994). Cowlishaw identified leopards as the primary predator of chacma baboons in his 1994 study, stating that leopards have been present at most every site where chacma baboons have been studied in Africa. Other studies have noted that chacma baboons manage to thrive in areas of high predator density because they employ

many anti-predator tactics, such as alarm calling, refuge use, and mobbing, as well as changing their group position, size, and spread (Cheney *et al.* 2004; Cowlishaw 1998; Ron *et al.* 1996). Chacma baboons will engage in these tactics differently in different areas and at different times, as leopards use certain regions more intensively than others, concentrating their movement in 'activity centers' within their home ranges and attacking prey most frequently in areas of dense or intermediate cover (Jenny and Zuberbuhler 2005; Zuberbuhler and Jenny 2002; Mizutani and Jewell 1998; Stander 1997; Karanth and Sunquist 1995; Bailey 1993). Furthermore, although the literature is inconclusive regarding which time of day leopards prefer to hunt, many studies have found leopards to attempt most of their kills at twilight and nocturnal hours (*e.g.* Martins and Harris 2013; Cowlishaw 1994), which may affect primate vigilance, habitat choice, and activity at these times.

The predator-prey dynamic between leopards and baboons, however, can be difficult to study. It is challenging to measure their encounter rates by way of direct observation due to leopards' cryptic nature and the unpredictability of where or when these events will occur (Chase Grey 2010). Thus, proximity data can provide an ideal mechanism for recording such contact patterns. By logging GPS locations whenever collared individuals interact with one another, proximity collars allow researchers to gather association data remotely and to avoid bias introduced by human observers.

Proximity data have rarely been used to answer questions related to predator-prey dynamics, however. More often, proximity collars are used to study intraspecies encounter rates and affiliative interactions, the rate of infectious disease spread, or mating systems (*e.g.* Maestas 2014; Boyland *et al.* 2013; Ralls *et al.* 2013; Vander Wal *et al.* 2013; Marsh *et al.* 2011; Prange *et al.* 2006; Ji *et al.* 2005). In reviewing the literature, I found only two instances of proximity

data use relevant to this study. Both studies deployed collars only within one species – lions in Tambling and Belton (2009) and wolves in Eriksen *et al.* (2007) – rather than in an interspecies manner as does this study. Additionally, the GPS collars used in this study are equipped with dual-action motion sensors, which measure acceleration along horizontal and vertical planes. Such activity data have been used in studying animals' daily activity patterns and hunting behavior, but never before to examine prey response to predator presence (Friebe *et al.* 2013; Martins and Harris 2013; Frölich *et al.* 2012; Eriksen *et al.* 2011). This study thus represents a fairly unprecedented method of studying the interactions between a prey species and its principal predator.

Although literature exists describing the effects of leopard predation risk on chacma baboon movement, habitat selection, and behavior, I was able to find only one study looking at all of these drivers synergistically or in combination with measured leopard activity (Bidner 2009). Bidner's (2009) dissertation, conducted in Loskop Dam Nature Reserve in South Africa, investigated the spatiotemporal patterns of leopards and baboons and determined the extent to which baboon anti-predator behavior corresponded with leopard movement patterns. Bidner (2009) found that most baboon-leopard encounters occurred in woodland habitats, that group spread was lowest in high-risk areas, and that vigilance and alarm calling were not related to leopard presence or absence. Although Bidner used telemetry data, she did not use proximity data and so could not consider interactions on a fine spatial scale. Moreover, regardless of methodology, the body of literature regarding primate-predator relationships and anti-predator strategies is scarce, has reached inconsistent conclusions, and usually focuses on low predator-density environments (Hill and Weingrill 2007). Therefore, this study aimed to strengthen the existing body of knowledge by investigating the extent to which leopard activity might influence

chacma baboon movement and behavior in the South Africa's Soutpansberg Mountain Range, where these two species' interactions represent a key predator-prey relationship.

In studying primate-predator interactions in the Soutpansberg, I addressed the overarching questions *To what extent might leopard activity correlate with baboon movement?* and *Do baboons behave differently in high-risk and low-risk areas?* As a precursor to answering these questions, I investigated during which times of day proximity events occurred most often, predicting that [1] leopards would preferentially hunt at crepuscular and nocturnal hours. Regarding my first question, I predicted that [2] baboons would exhibit a preference for open and rocky habitats and leopards dense ones, and that leopard-baboon encounters would most frequently occur in dense habitats. I also predicted that [3] baboon ranging behavior would change after a leopard encounter, with group size constricting and activity increasing after a proximity event. Regarding my second question, I predicted that baboons would exhibit different behaviors in areas where predation events were more likely, [4] exhibiting higher scanning rates in dense habitats than in open and [5] scanning more and foraging and engaging in social behavior less in areas with high measured leopard activity.

Methods

Study Site

I considered data collected between March 2013 and August 2015 at Lajuma Research Centre, which is located in the western portion of the Soutpansberg Mountains in South Africa's Limpopo Province (23°02'17.1"S 29°26'26.5"E, Figure 1). The study site is mountainous, ranging in elevation from 1150 to 1750 m. Climate is temperate, with a warm, wet summer season between October and March and a cool, dry winter season from April to September (Willems 2007). Vegetation in the area comprises various habitat types, such as forest, thicket, savanna, and grassland (von Maltitz 2003). Mean annual rainfall averages 724 mm and mean annual temperature is 17.1 degrees C (Willems *et al.* 2009). Lajuma's variety of microclimates and microhabitats gives rise to high diversity: the Soutpansberg hosts over 60% of South Africa's mammal species, with an especially diverse predator assemblage (Gaigher and Stuart 2003). Although leopards are baboons' primary predators at Lajuma, other predator species include crowned eagles (*Stephanoaetus coronatus*), verreaux's eagles (*Aquila verreauxii*), rock pythons (*Python sebae*), and spotted hyenas (*Crocuta crocuta*) (Seiphetho 2014).

My study was a part of Durham University's long-term data collection with the Primate and Predator Project, which was established in 2011. The project is assessing the role of montane environments in conservation in part by investigating predator-prey interactions. Hill and Williams study three species of primate – samango monkeys (*Cercopithecus mitis erythrarchus)*, vervet monkeys (*Chlorocebus pygerythrus*) and chacma baboons – and many predator species. While present at the field site between June and August 2015, I helped collect all categories of data considered in this study; other research assistants collected data from outside this time span.
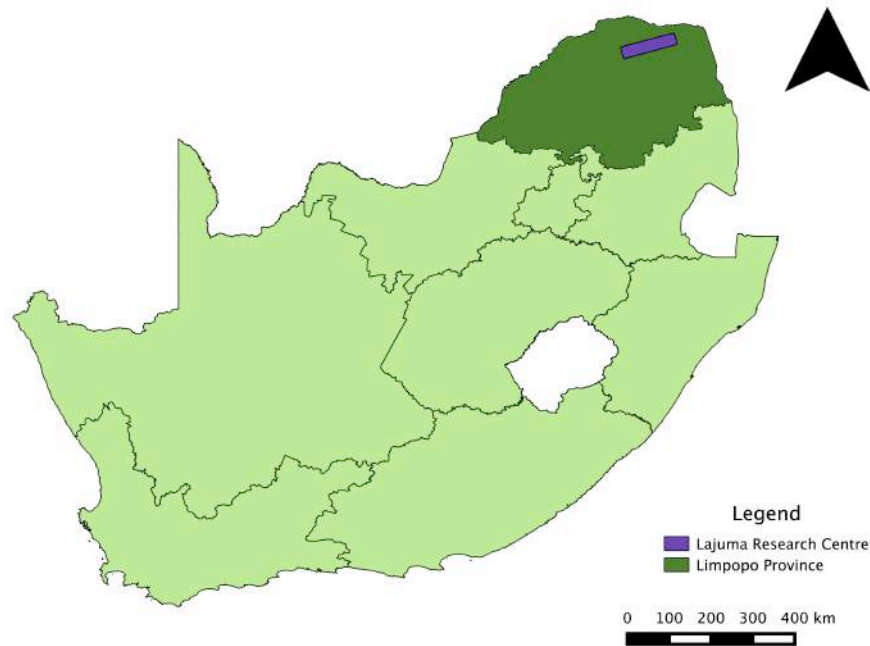
Figure 1. The study area: the location of the Limpopo Province in South Africa and Lajuma Research Centre in purple.

Study Species

Chacma baboons are highly social primates that live in groups of 10 to 130 individuals (Hoffmann 2008). They are opportunistic and omnivorous feeders and are found in savanna woodland, steppes, sub-desert, montane, cape fynbos, and succulent karoo habitats throughout southern Africa (Seiphethlo 2014). Baboons have large home ranges and long daily path lengths in comparison with other primate species (Milton and May 1976). As a ubiquitous and largely terrestrial species, baboons might seem an obvious choice for many predators, but their large teeth, alarm barks, and mobbing capabilities prevent them from being a preferred prey species for many carnivores (Hart 2000).

The study site hosted a habituated baboon troop consisting of approximately 100 individuals. There were also several other unhabituated baboon troops in the area. Research assistants have collected scan data and GPS data on the former troop since a PhD student

habituated them in 2007. The baboons' ranging area during my study period was 48.59 km^2 (Figure 2; Appendix).

Leopards are extremely adaptable generalists that are widely distributed throughout Africa and Asia (Bailey 1993; Bothma 1989). They have the largest habitat tolerance of the Old World felids, residing in a variety of different habitats, from deserts to forests (Henschel 2008). Their diet is also extremely variable and includes close to 100 species in sub-Saharan Africa (Henschel 2008). Leopards in the study area are known to prey upon baboons, as evidenced by scat analysis and observed predation events (C. Howlett and K. Williams, pers. comm.). In accordance with leopards' preference to hunt in regions with dense or intermediate cover, leopard density tends to be higher in forested sites and lower in more open sites (Bothnia and Le Riche 1986). Home range estimates for leopards vary from as little as 100 km^2 to over 1000 km^2, with males having larger home ranges than females (Bailey 1993). Leopards are a cryptic species, elusive and largely nocturnal, which can make obtaining data on their behavior difficult (Chase Grey 2010).

Researchers have monitored Lajuma's leopard population via camera traps and GPS collars since 2011 (Primate and Predator Project 2013). Eight leopards have been collared at Lajuma since June 2012, six males – Drogo, Anakin, Michel, BB, O'Malley, and Pimms – and two females – Jenny and CC. The leopards' ranging area over my study period was 153.05 km^2 (Figure 2; Appendix).
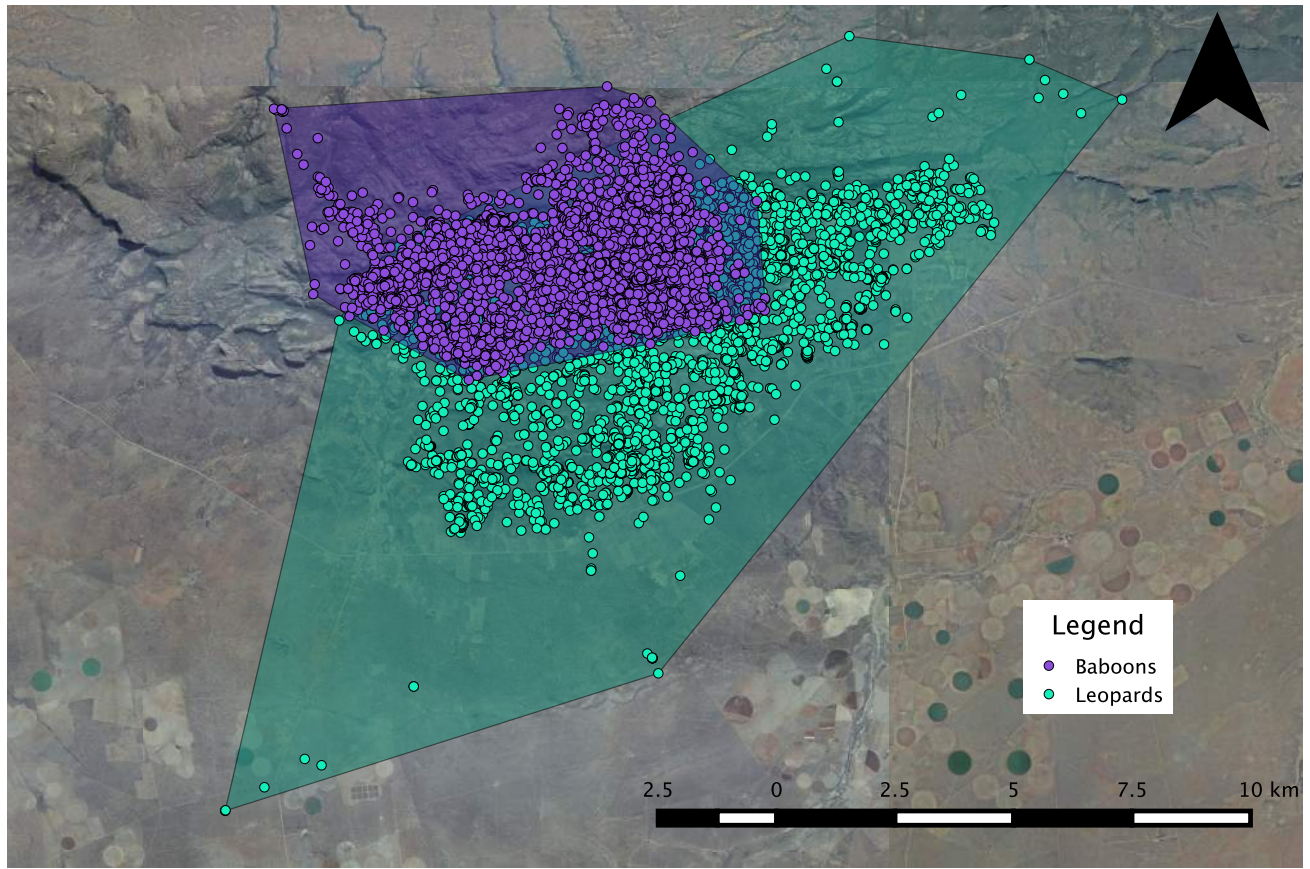
Figure 2. Minimum convex polygons showing the extent of baboons' (purple, 48.59 km^2) and leopards' (blue, 153.05 km^2) ranges at the study site, as well as their overlap. Each dot represents the location of a collared animal. Data are from GPS-collared baboons and leopards between June 2013 and June 2015.

GPS, Proximity, and Activity Data

Leopard Data Collection

I used GPS Plus collar data from VECTRONIC Aerospace, Berlin, Germany, to determine movement patterns and habitat preferences of collared leopards. These data consisted primarily of GPS collar data collected by research assistants between June 2012 and June 2015. This study used data from two collared leopards, a female named Jenny and a male named BB, in proximity analyses and data from an additional leopard, Pimms, in other analyses (Table 1). I

considered leopards in the study only if their collars provided at least a year of continuous GPS data. I excluded Pimms from proximity analyses due to technical issues with his proximity logger and because he was killed by a snare before the end of the study period. Researchers used a VHF transmitter to locate these leopards and a UHF device to download data from the collars. The collars recorded leopard GPS locations every 3 hours and 20 minutes, with each GPS coordinate called a fix. Collars automatically dropped off the study animal at the end of 455 days.

Table 1. Data collection period for each of the four collared leopards.

Collar Number	Individual	Date Collared	Collar Drop Off	Date Died	Days Collared
10011	BB	6/12/13	3/19/14	NA	280
10012	Jenny	9/20/13	8/14/14	NA	328
10009	Pimms	7/18/14	NA	6/16/15	333

In addition to taking GPS fixes, the leopard collars communicated with UHF-ID tags on the baboon GPS collars to record proximity events, indicating when a collared baboon was within around 60 meters of a collared leopard (Williams and Williams 2014; Figure 3). I used this information to measure how the troop reacted to leopard approach and presence. Collars recorded proximity points every 20 minutes after an event began as long as the leopard remained within 60 meters of the GPS collared baboon (Williams and Williams 2014).
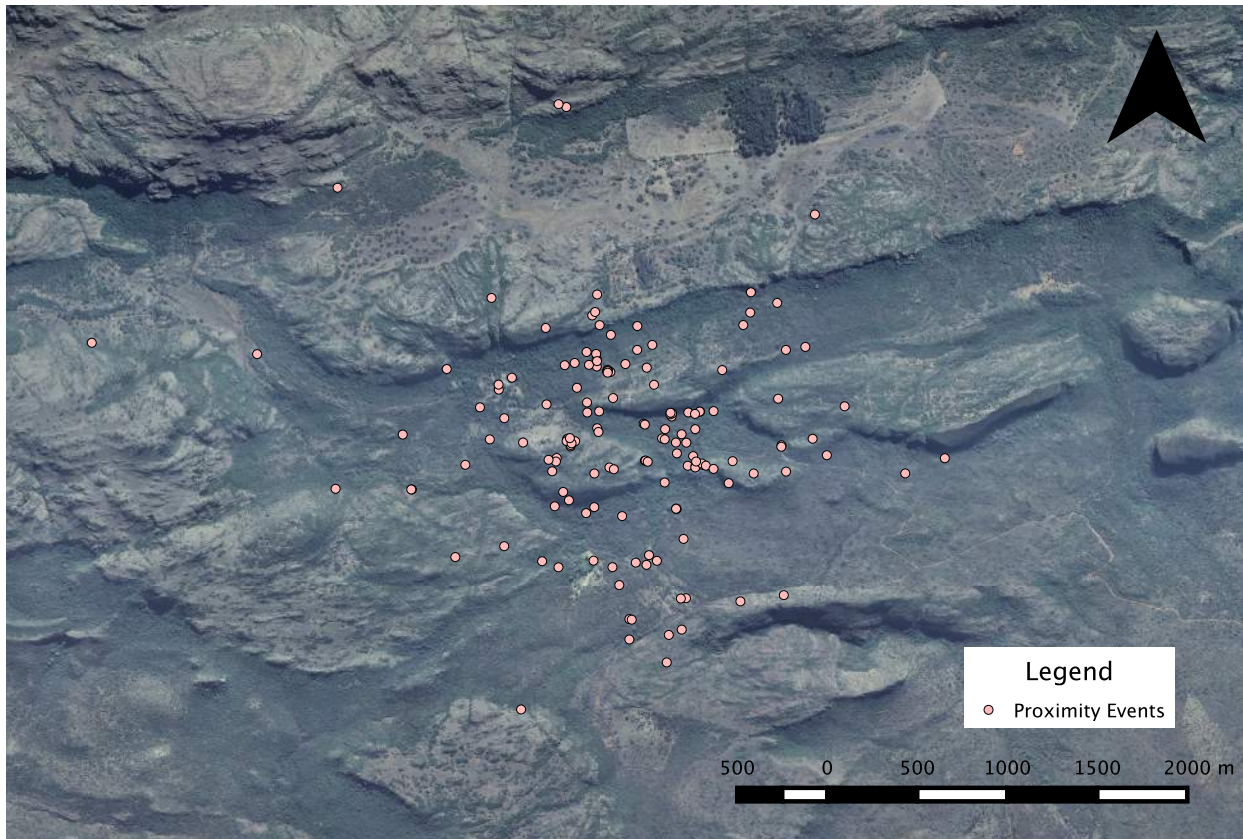
Figure 3. Map of baboon-leopard encounters, with each pink dot representing a proximity event. Data are from a GPS-collared baboon and leopard at Lajuma Research Centre in South Africa's Limpopo Province from June 2013 to June 2015.

Baboon Data Collection

I considered baboon GPS data from March 2013, when Lajuma researchers first fitted an individual with a GPS collar, until August 2015, when I left the field site. The research center had collared two baboons in the past two years, a female named Lobelia once and another female named Melissa twice (Table 2). Unlike with the leopard data collection, there were no complications with the baboon GPS data during the study period. Collars recorded baboon GPS positions every hour between 06:00 and 20:00 local time, with an additional fix taken at 00:00 to show sleeping sites.

In addition to GPS collaring two baboons, Lajuma researchers fitted four additional individuals with proximity collars starting in September 2013 – Mangle, Boxy, Yolanda, and

Earhart (Williams and Williams 2014). These proximity collars communicated with GPS collars to provide information about how close troop members were to the GPS collared baboon at any given time, allowing me to calculate group spread. The collars logged baboon proximity information every five minutes as a number between -40 dB and -130 dB, recording proximity data between the hours of 03:30 and 18:00 local time.

Apart from recording GPS locations and proximity, these collars also measured activity. They were equipped with an acceleration sensor that continuously measured activity on two axes. The collars recorded averages of these measurements at two-minute intervals as a unitless number between 0 and 255. The sensors were oriented perpendicular and parallel to the animal's spine, so horizontal and vertical movements generated x and y values, respectively. I used this data to determine baboon movement after leopard encounters.

Table 2. Data collection period for each of the two collared baboons Melissa was collared twice.

Collar Number	Individual	Date Collared	Collar Drop Off	Days Collared
11940	Lobelia	3/9/13	2/5/14	333
11942	Melissa 1	7/27/14	4/30/15	378
11938	Melissa 2	6/4/15	Currently Collared	81

Baboon Behavioral Data Collection

Behavioral data consisted of scan data and manually recorded GPS points. Two research assistants followed the troop, conducting 10-minute scan samples at 10-minute intervals. Assistants recorded the behavior of as many individuals as possible across all age-sex classes within this window, systematically moving within the troop throughout the day to sample a variety of individuals. In this study, I considered all behavioral data collected between April

2014 and July 2015, as vigilance data only started being collected consistently after the spring of 2014.

I used scan data from the following categories: age-sex class, habitat type, and vigilance. The eight habitat categories were woodland, forest, rock, road, farm, bush, grassland, and marshland (Figure 4). I also considered five categories of vigilance and four categories of activity, each with several sub-categories (Table 3). In order to be recorded, behaviors were required to last 5 seconds or more. Only adult baboons were considered in analyses, as studies have found infant and juvenile primates to exhibit lower vigilance levels than adults, possibly because they rely on older troop members to scan for them (de Moura and Alonso 2000, Savage *et al.* 1996, Peres 1993). Researchers recorded GPS data at the end of each scan.
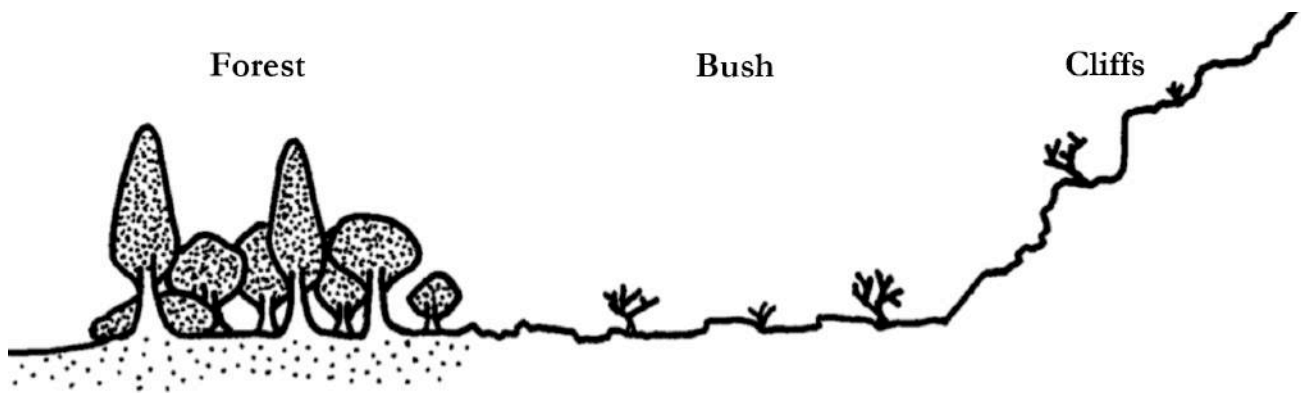
Figure 4. An example of closed and open habitat, as well as one type of refuge – cliffs (Cowlishaw 1997).

Table 3. The six categories of vigilance behavior and two categories of foraging and social behavior recorded during scan samples.

Behavior	Qualifiers	Definition
Vigilance	Not vigilant	
	Looking up	
	Looking down	
	Scanning	Looking back and forth in a horizontal plane; associated with detecting predators
	Social vigilance	Looking at another troop member
	Observer	
Foraging		Searching for food
	Feeding	Actively chewing and ingesting food
Social	Grooming	
	Aggression	Individual involved in an antagonistic display

Data Analysis

GIS Analysis

I used QGIS (version 2.12.0-Lyon) to define both home ranges for the study individuals and the habitats constituting these ranges. I delineated six habitat types for the entire study area in GIS to answer habitat-preference questions: forest (closed canopy), bush (intermediate cover), open savanna, cliffs, rocky vegetation, and anthropogenic (human settlements or agriculture). Due to time limitations and the level of detail of the satellite images, it was necessary to use this simplified list of habitats rather than the same eight collected in the field. I used satellite images obtained from National Geo-Spatial Information at the South African Department of Rural Development and Land Reform in 2012 to classify which habitats fell into the leopards and baboons' ranges by drawing polygons over distinct landscape features and calculating residence times within each habitat type. I used the T-LoCoH package in R (version 0.98.1028 2009) to examine home ranges and high-use areas using local convex hull analysis (Getz *et al.* 2007). I defined 'high-use areas' as having an isopleth level between 0.1 and 0.5.

In my analyses, I considered only proximity events with at least hour-long intervals in between one fix and the next. I performed a chi squared for differences test to determine at which time of day proximity events occurred most. I categorized the events as diurnal (07:00-17:00), nocturnal (18:00-07:00), and crepuscular (06:00-07:00 and 17:00-18:00) based on the average annual sunrise and sunset times at the research center. I calculated expected proportions for each event by dividing the number of hours comprising each window by 24 hours and compared these with the observed proportions.

I performed a simulation test to determine which habitats leopards and baboons displayed preference for as well as in which habitats proximity events occurred most. I calculated residence times within each habitat for each of these three categories to determine the observed proportions. To determine the expected values, I calculated the proportion of each species' range made up by each habitat type.

I performed paired *t*-tests to determine whether baboons changed their ranging behavior upon coming into close proximity with a GPS collared leopard. To do this, I examined the extent to which average group spread and activity differed before and after a proximity event. I calculated group spread by averaging the collars' proximity signal strengths within a given time interval. I considered hour-long intervals on either side of the proximity event to determine if group spread or activity differed, excluding from analysis any events that did not have sufficient data both before and after the event occurrence. I also excluded from the group spread analysis any events occurring during hours when the baboon collars were turned off and any events occurring before all four baboons were fitted with proximity collars. I considered activity

measurements from the x and y axes separately because there was a significant difference in the activity measured along each axis ($t_{2554,2} = 16.62$, $p<0.01$, 95% CI [2.85 3.61]).

I again used chi squared for differences tests to detect differences in baboon vigilance behavior between areas of high and low leopard predation risk. First, I examined scanning rates in each of the nine habitats to determine if they differed. I calculated the proportion of scans occurring within each habitat by dividing the number of scans occurring in each habitat by the total number of vigilance behaviors. I calculated standard error as a means of *post hoc* analysis to discover which habitats in particular had significantly different scanning rates. I excluded the habitat category 'other' in my analyses, as well as behaviors during which researchers recorded individuals at a border between habitats. For the purposes of these analyses, habitat was sufficiently defined 98.3% of the time. I also investigated whether scanning, social, and foraging behavior differed between areas of high and low measured leopard activity. To do this, I calculated the proportion of behaviors recorded in and out of high-use areas and compared them using two-sample difference of proportions *z*-tests.

Results

Proximity-Event Timing

There were 773 proximity fixes over the course of the yearlong study period and 160 of these met the criteria to be defined as proximity events. Proximity event occurrence was not homogenous across time of day (Figure 5; $X^2_{(2)} = 136.3$, $p<0.01$). Proximity events occurred significantly more than expected during the night (65.4%; 95% CI [62.5% 68.5%]) and significantly less than expected during the day (28.3%; 95% CI [25.4% 31.2%]).
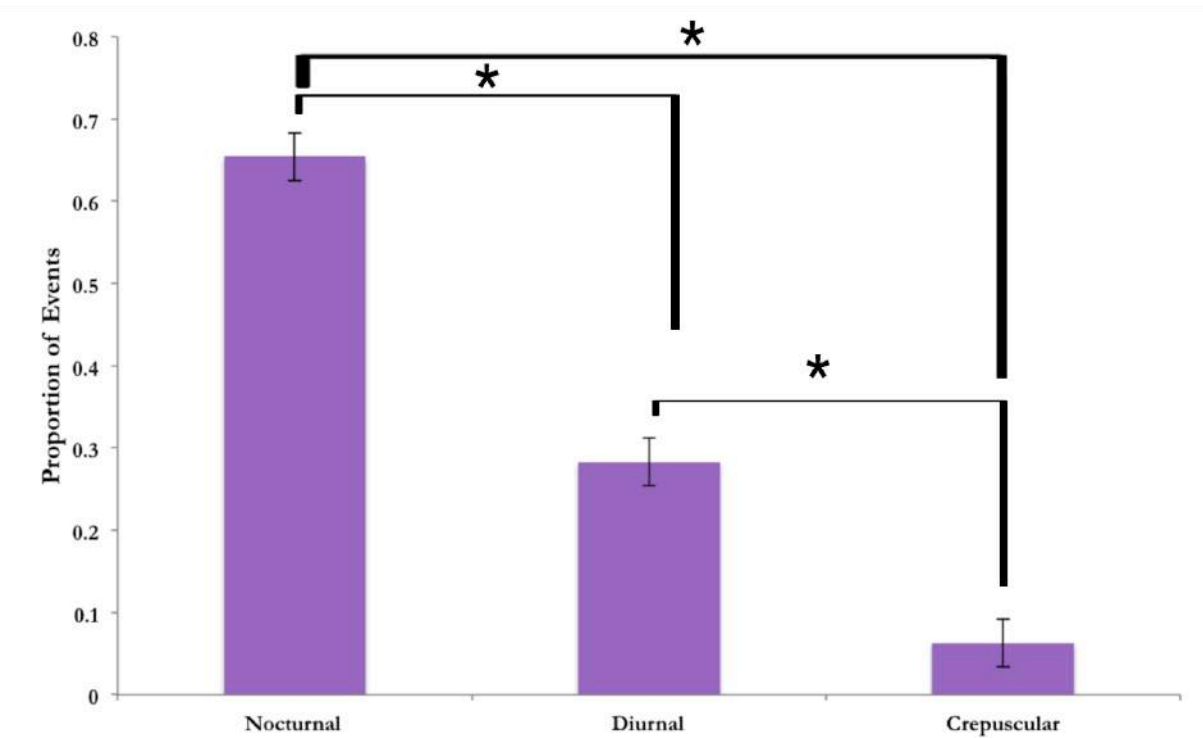
Figure 5. The proportions of nocturnal, diurnal, and crepuscular proximity events (± Standard Error). Asterisks indicate a significant difference ($X^2_{(2)} = 136.3$, $p<0.01$) between the proportions of events falling within each time period. Events occurred more often than expected at night and less often than expected during the day. Data are from a GPS-collared baboon and leopard at Lajuma Research Centre in South Africa's Limpopo Province from June 2013 to June 2015.

Habitat Preferences

Baboons were found on cliffs significantly more frequently than were leopards – 25.1% (95% CI [19.7% 30.5%]) versus 4.2% (95% CI [3.9% 5.0%]) of the time (Figure 6). Leopards were found in forested habitats significantly more frequently than were baboons – 53.5% (95% CI [49.8% 57.2%]) versus. 32.4% (95% CI [30.8% 34.0%]) of the time. The two species showed similar preference for bush and anthropogenic habitats.

Proximity events occurred significantly more frequently than expected in bush habitats (22.9%, 95% CI [15.1% 30.7%]) and significantly less frequently than expected in open savanna habitats (3.8%, 95% CI [-2.0% 9.7%]; Figure 7).
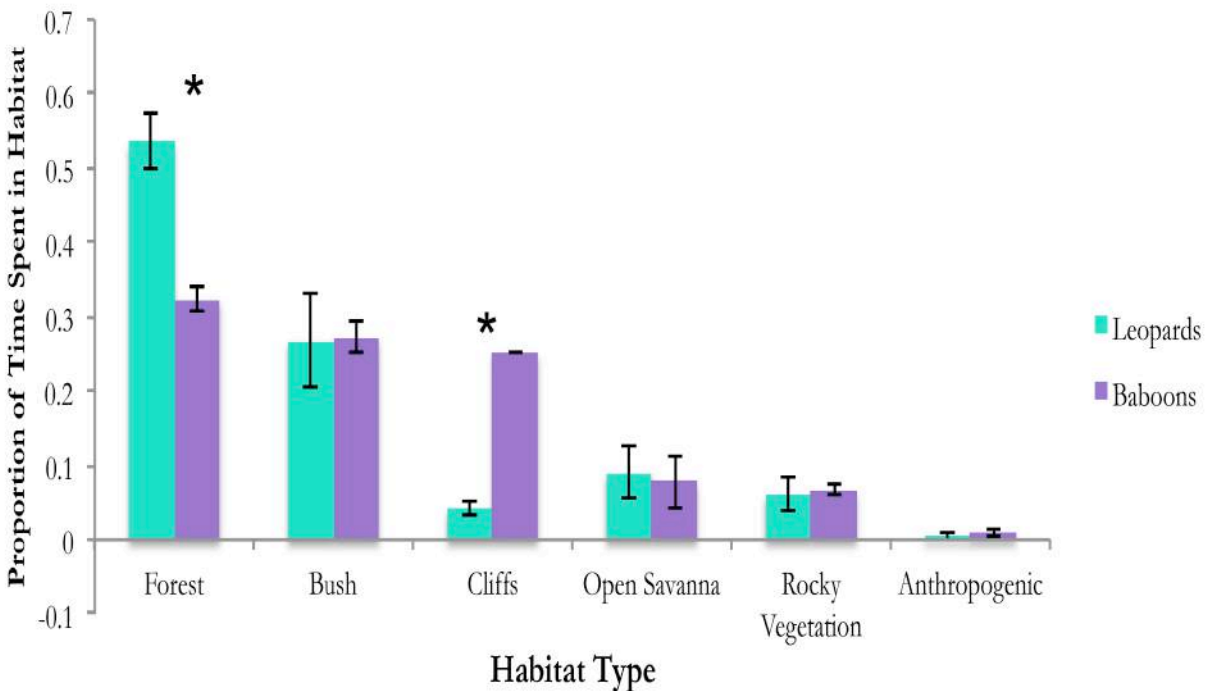
Figure 6. Proportion of GPS fixes for leopards and baboons occurring in each of six habitat types: forest, bush, rocky vegetation, cliffs, open savanna, and anthropogenic (± Standard Error). Leopards were found in forested habitats more frequently than baboons and baboons were found on cliffs significantly more than leopards. Asterisks denote statistical significance. Data are from a GPS-collared baboon and leopard at Lajuma Research Centre in South Africa's Limpopo Province from between June 2013 and August 2015.
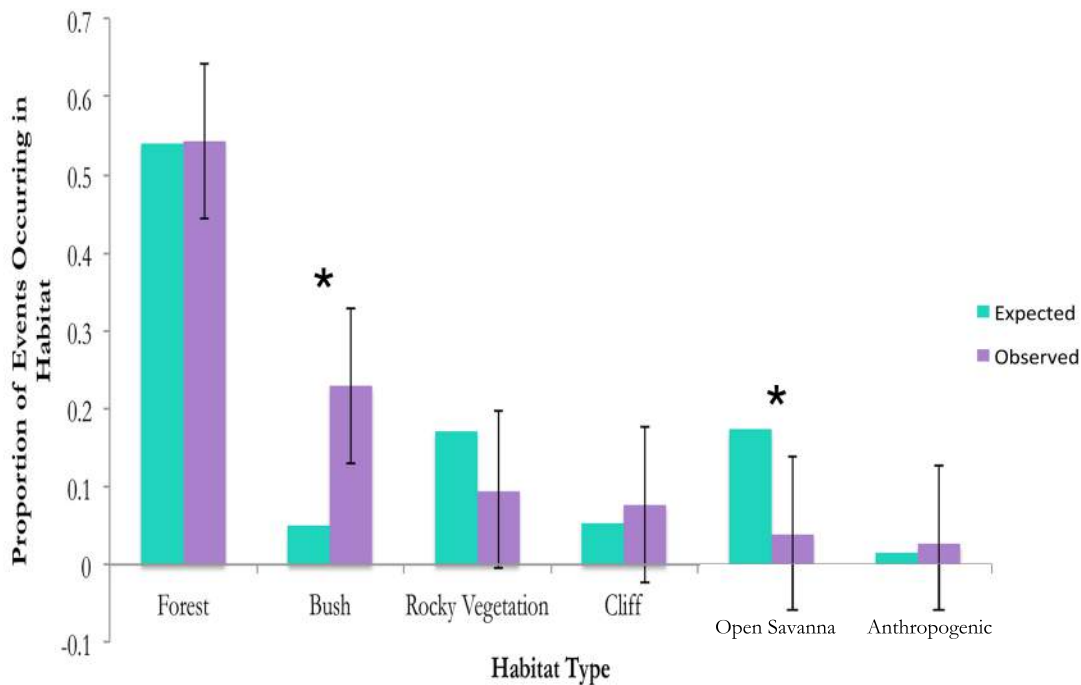
Figure 7. Proportion of proximity fixes occurring in each of six habitat types: forest, bush, rocky vegetation, cliffs, open savanna, and anthropogenic (± Standard Error). Proximity events occurred significantly more than expected in bush habitats and significantly less than expected in open savanna habitats. Asterisks denote statistical significance. Data are from a GPS-collared baboon and leopard at Lajuma Research Centre in South Africa's Limpopo Province from between June 2013 and June 2015.

Baboon Response to Leopard Proximity

Baboon activity was significantly higher after a proximity event occurred on both the X ($t_{2554,2} = 9.2$, *p*<0.01, 95% CI [-10.3 -6.7]) and Y ($t_{2554,2} = 8.75$, *p*<0.01, 95% CI [-8.5 -5.4]) accelerometer axes. The troop's group spread did not exhibit this trend; there was no significant difference in baboons' average group spread before and after a proximity event ($t_{121,2} = 1.3$, *p*=0.19, 95% CI [-0.6 3.0]).

21
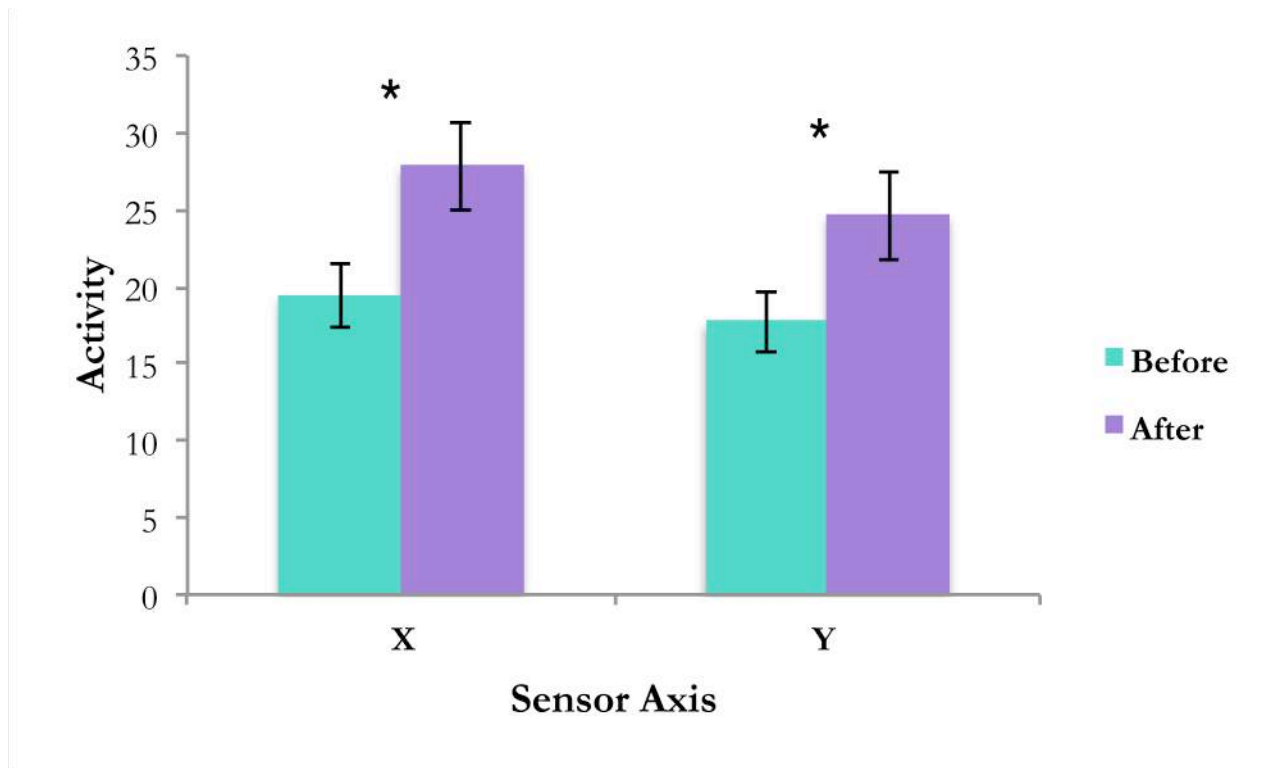
Figure 8. Baboon activity along the sensor's X and Y axes measured from GPS collar sensors before and after a proximity event (± Standard Error). Baboons were significantly more active after a proximity event. Asterisks indicate statistical significance. Data are from a GPS-collared baboon and leopard at Lajuma Research Centre in South Africa's Limpopo Province from between June 2013 and August 2015.

Baboon Vigilance, Foraging, and Social Behavior

Baboon vigilance varied across different habitats ($X^2_{(47)} = 179.89$, $p<0.01$; Figure 9). The proportions of scanning behavior occurring in grassland (32.6%, 95% CI [31.6% 33.6%]), rocky (10.5%, 95% CI [9.9% 10.5%]), farm (8.0% 95% CI [8.9% 7.1%]), and road (9.2%, 95% CI [8.7% 9.8%]) habitats were significantly higher than expected, whereas they were significantly lower than expected in forest (3.4%, 95% CI [2.9% 3.8%]) and bush (6.3%, 95% CI [5.9% 6.8%]) habitats.
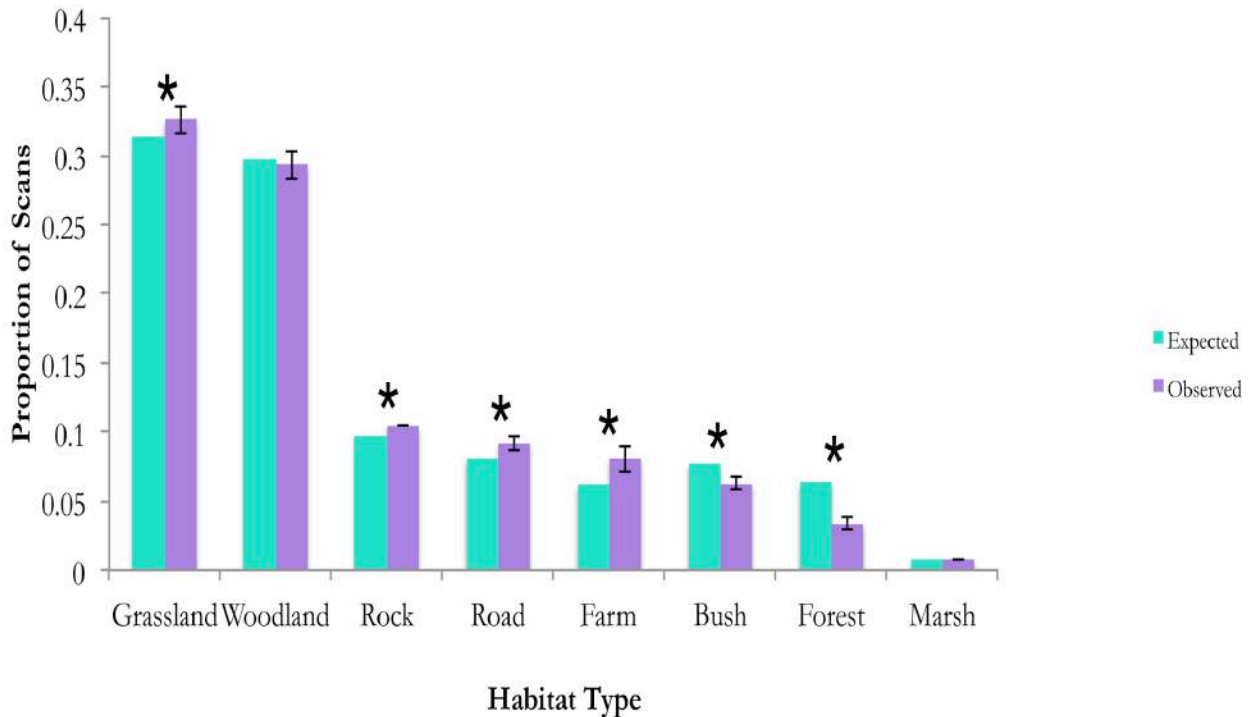
Figure 9. Proportion of scanning behavior occurring in each of eight habitats: grassland, forest, woodland, rock, farm, bush, road, and marshland (± Standard Error). Baboons scanned significantly more than expected in grassland, rocky, farm, and road habitats and significantly less than expected in forest and bush habitats. Asterisks indicate statistical significance. Data are from baboon behavioral scans collected between April 2014 and August 2015.

Peaks in vigilance occurred in areas of high measured leopard activity (Figure 10). Baboons exhibited a significantly higher proportion of scanning behaviors inside of high-use leopard areas than outside of them – 21.7% versus 24.7% ($z=2.61$, $p<0.01$; Figure 11). Social vigilance exhibited this same trend, with 10.72% of social vigilance behaviors occurring inside of high-use areas and 7.2% occurring outside of them ($z=6.10$, $p<0.01$). Baboons spent a higher proportion of time not vigilant outside of high-use areas than inside of them – 53.7% versus 47.9% ($z=5.67$ $p<0.01$). Baboons engaged in social behavior significantly more ($z=2.02$, $p=0.022$) and foraged significantly less ($z=4.66$, $p<0.01$) in high-use versus low-use leopard areas.

Figure 10. T-LoCoH analysis of the three GPS-collared leopards considered in this study (k=24). Redder areas are more intensely used. Iso level refers to the density isopleth of the area, a reflection of where an animal spent the most time. Data are from GPS-collared leopards at Lajuma Research Centre in South Africa's Limpopo Province from between June 2013 and June 2015.

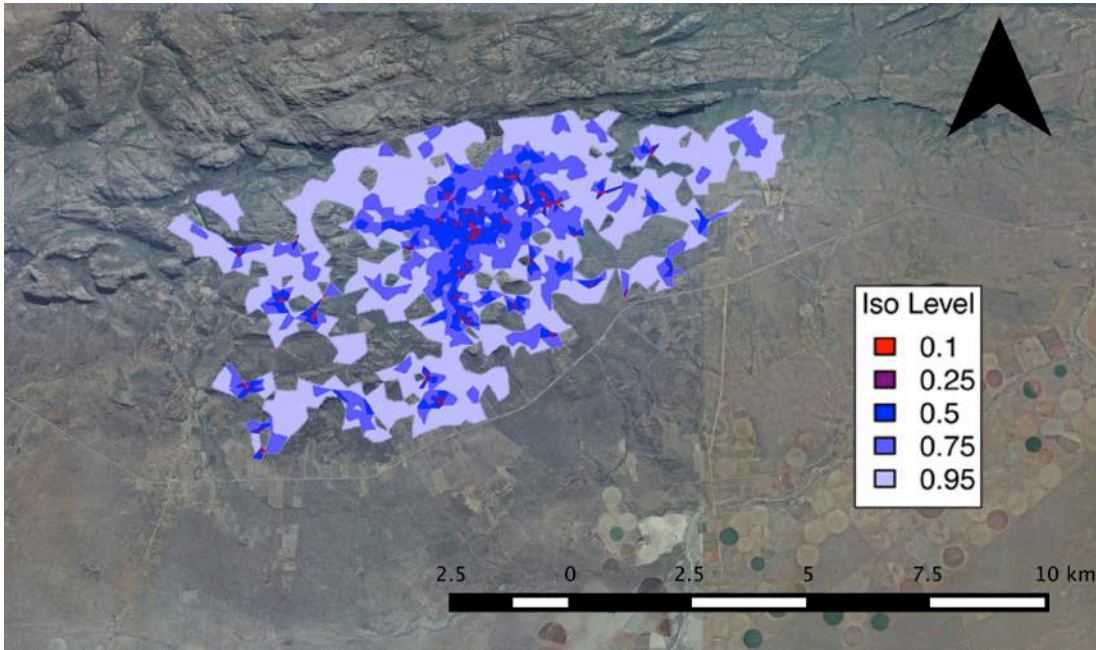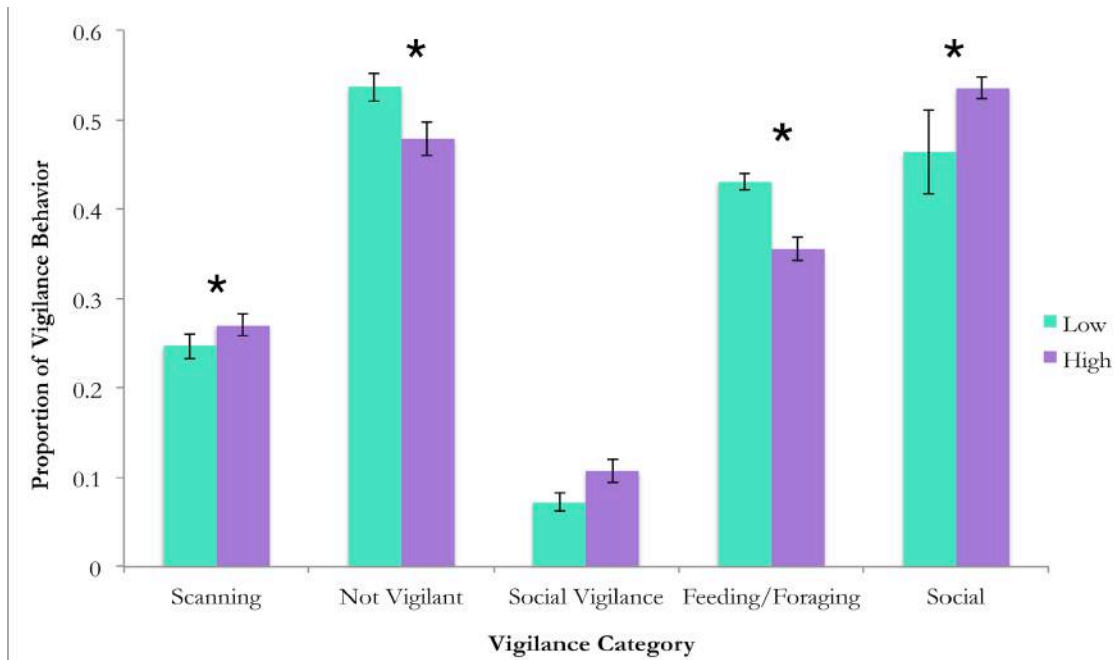**Figure 11.** Proportion of time spent scanning, not vigilant, socially vigilant, foraging, and engaging in aggressive encounters and grooming in high- and low-use leopard areas (± Standard Error). In high-use leopard areas, baboons were more vigilant than expected, foraged less frequently than expected, and exhibited more social behaviors than were expected. Asterisks indicate statistical significance. Researchers collected scan data at Lajuma Research Centre in South Africa's Limpopo Province between January 2015 and August 2015.

24

Discussion

This study investigated the relationship between leopard movement patterns and chacma baboon behavior within South Africa's Soutpansberg Mountain range. By examining the interactions between these two species using GPS, proximity, activity, and behavioral data, I hoped to gain an understanding of a cryptic predator's hunting strategies and its prey's defenses. When I considered baboon reactions to leopard presence, I found significant correlations between leopard activity and baboon anti-predator responses in the Soutpansberg.

Proximity-Event Timing

Proximity events were not distributed evenly throughout the day; they occurred significantly more frequently nocturnally than diurnally, which may indicate that leopards preferentially hunt at night. Cowlishaw (1994) observed that leopard attacks were most likely to succeed at sleeping sites where prey maneuverability was reduced. It is logical, then, that leopards would maximize capture success by hunting at night when the entire troop is resting on precarious rocky terrain. In combination with intense darkness, these conditions provide a window of opportunity for predation. It is important to note, however, that the literature is inconsistent when it comes to defining what times leopards prefer to hunt, and some studies have found most kills to occur during daylight hours (Pitman 2013; Cowlishaw 1998).

It is important to recognize that although I am considering proximity events as a proxy for predation, successful or attempted, some of them could instead indicate leopards and baboons moving within the same vicinity but not interacting. Taking this into consideration, it is possible to argue that proximity events preferentially occur at night because leopard activity peaks at this

time (Ngoprasert 2007). If these are the times leopards are moving most, then naturally they are the times that leopards are more likely to be involved in interspecific encounters.

Habitat Preferences

The result that baboons exhibited a stronger preference for cliffs than did leopards and that leopards exhibited a stronger preference for dense habitats than did baboons largely supports my hypothesis. As ambush predators, leopards would be expected to frequent habitats which provide them with greater cover. In response to this, baboons might exhibit an aversion to these closed habitats, instead preferring to frequent steep, rocky habitats that leopards have difficulty accessing. The system considered in this study is too complex to be able to verify that this mechanism is at play, however, and it is important to keep in mind that such conclusions should not be generalized to other baboon and leopard populations. Although some studies have found similar trends in baboon and leopard habitat preference (Hayward *et al.* 2006; Bailey 2005; Cowlishaw 1997; Hes 1991), other studies have found both species to prefer habitats with intermediate cover (Bidner 2009; Balme *et al.* 2007). The behaviors of African leopard and baboon populations are too variable to allow researchers to make statements about the species as a whole from individual studies.

The literature more concretely supports the result that proximity events occurred more frequently than expected in bush habitats and less frequently than expected in open habitats. Although researchers debate in which habitat it is optimal for leopards to hunt, I found no disagreement in the literature that the smallest proportion of successful prey captures occurred in open habitats, likely because there is not enough cover for approaching leopards to hide from their targets. It follows that leopards would be unlikely to execute a predation attempt in open

areas and thus that the smallest proportion of proximity events would occur in this habitat. There is also widespread support for the idea that predation attempts preferentially occur in bush habitats. Balme *et al.* (2007) found that leopards favored intermediate habitats for hunting. He rationalized that this was true because in extremely dense habitats, a leopard's view of its prey is reduced, as is the leopard's ability to chase its prey. He proposed that intermediate habitats provide the optimal middle ground for predation, with enough cover to obscure the predator as it stalks its target, but not too much to hamper the capture process. This finding deviates from my hypothesis that leopards would preferentially hunt in dense habitats, such as forests; however, there is a great deal of support for the idea that leopards show preference for dense habitats in previous studies (Hayward *et al.* 2006; Bailey 2005; Cowlishaw 1993; Altmann and Altmann 1970). That I did not find proximity events to occur in forested habitats significantly more than expected could be attributed to the fact that vast majority of habitat defined in the study was forest, and an extremely high proportion of proximity events would have had to occur in this habitat to produce a significant result.

Baboon Response to Leopard Proximity

The GPS-collared baboon's increase in movement following a proximity event could be attributed to several factors. The baboon might have increased its pace, from resting to walking or walking to running, to move away from the leopard. The higher activity reading could also indicate that the baboon began to move its head around more, sensing the leopard's presence and investigating its surroundings to assess the level of threat and determine if further response is needed. Unfortunately, the collars sensed motion in only two directions and thus were able to detect only general activity patterns. It may be fruitful for future studies to use activity sensors

that measure acceleration on three axes and can therefore distinguish among particular behaviors. This would give researchers an even clearer idea of how baboons alter their movement patterns in response to perceived predation threat.

In contrast with Bidner (2009), who found baboons' group spread to be lower in high-risk leopard areas, group spread did not constrict significantly following a predation event in this study. There are three possible reasons for this: (1) that the group spread data was too inconsistent to reveal any trends, (2) that altering group spread in response to leopard presence is not an adaptive anti-predator strategy in this environment, or (3) the baboons fail to realize that a leopard is nearby and thus do not react. Regarding the first possibility, after excluding events that did not have sufficient data before and after the event occurrence or that occurred at night when the collars were off, I was able to use only 11% of proximity events in group spread analyses. As nocturnal proximity events occurred more frequently than diurnal ones, this lack of data likely influenced the results. Furthermore, I was oftentimes able to use only two or three individuals in calculating group spread; four would have provided a more accurate average (S. Williams, pers. comm.). Potentially, if more reliable data were collected and considered in analysis, the finding would be similar to Bidner's (2009).

This result could also be attributed to a lack of baboon response to leopard presence. Matsumoto-Odo (2015) observed that although a troop of chacma baboons emitted alarm calls both preceding and following a leopard predation event, they exhibited no other response. This observation is supported by other literature. Some studies have preliminarily found that baboons may be relatively unresponsive to predation risk in terms of group dynamics (Cowlishaw 1996), as they live in large groups where they feel safer, and as they employ other anti-predator behaviors such as refuge use (Martins and Harris 2013; Hayward and Slotow 2009; Ngoprasert

28

2007; McManus 2009; Cowlishaw 1996; Cowlishaw 1994; Bailey 1993). If employing anti-predator strategies such as reducing group spread is not necessary to reduce capture risk, then engaging in these behaviors might not be an adaptive use of baboons' time.

Regarding the third possibility, Bidner (2009) found that baboon proximity to GPS-collared leopards may have had a weaker influence on the troop's group spread than did proximity to leopard scats and tracks, presumably because the baboons noticed these signs more easily than they could a stealthy leopard. Perhaps had I considered such leopard signs rather than proximity events, starker group spread differences would have emerged.

Baboon Vigilance, Foraging, and Social Behavior

In general, baboon scanning behavior did not align with probable predation risk. Despite leopards' tendency to hunt in intermediate and dense habitats and my finding that proximity events primarily occurred in bush habitats, baboons were less vigilant than expected in forest and bush habitats. In addition, baboons displayed heightened vigilance in the supposedly 'safe' grassland habitat. Although these results contradict my predictions, they are not entirely surprising, as past studies have found inconclusive relationships between baboon vigilance and habitat type (Bidner 2009; Hill and Cowlishaw 2002; Cowlishaw 1998).

My finding suggests that perception of risk in this habitat might be influenced by other factors. Perhaps baboons base their vigilance behavior more upon risk related to birds of prey, snakes, or humans. For example, I would imagine the higher scanning rates in farm and road habitats to have more to do with human-wildlife conflict than predation risk. Human-baboon conflict at Lajuma is relatively prevalent; the owners of several neighboring farms often try to shoot baboons that roam onto the farmers' properties (K. and S. Williams, pers. comm.).

Furthermore, baboons did not reduce affiliative behaviour, such as grooming and aggression, in high-risk areas as predicted. Cords (1995) found vigilance rates of individuals engaging in affiliative behavior to be significantly lower than those of resting or foraging individuals, suggesting that grooming was a risky activity. In contrast with this result, my finding suggests that vigilance and grooming may not always be trade-offs – an increase in one of these behaviors may not necessitate a decrease in the other. Perhaps baboons groomed more in high-risk areas as a stress-reduction technique, as has been found in past research on baboons and other Old World monkeys (Roubova *et al.* 2015, Wittig *et al.* 2008, Aureli *et al.* 1999). It is also possible that the observed increase in social behavior was associated with factors other than predation risk or was due to chance.

Baboons also exhibited certain behaviors supporting the idea that they might have an accurate perception of predation risk. Although baboons did not scan significantly more than expected on cliffs, they did exhibit slightly higher scanning rates in this area. Baboons could be conditioned to associate these habitats with leopards' predilection for capturing baboons as they approach sleeping sites, which are most often rocky cliffs (Bidner 2009; Cowlishaw 1994, Anderson and McGrew 1984). Their heightened vigilance in this habitat could be a pre-emptory response to this sensed risk.

Additionally, peaks in baboon vigilance and lowered foraging rates occurred in areas of high leopard activity. The increase in social vigilance could be attributed to adult females' tendency to exhibit heightened vigilance in conditions that threaten their infants (Treves *et al.* 2003), such as regions favoured by predators. By significantly increasing their scanning at the expense of foraging in high-use leopard areas, baboons might be investing more in predator detection than in nutrition acquisition in places where they are more likely to be preyed upon. In

agreement with this, Bidner (2009) also found that baboons foraged less frequently in high-use leopard areas than in low-use areas, and many studies on other primates have found evidence for predation-risk sensitive foraging (*e.g.* Barnett *et al.* 2012, Teichroeb and Sicotte 2011, Cowlishaw 1997, de Ruiter 1986).

Limitations

There are several limitations to this study. One is its small sample size. Hundreds of thousands of data points were recorded over the course of the study, but these data came from only two leopards and two baboons. It is possible that these collared individuals were exhibiting anomalous behavior with regard to how the majority of individuals act. It is also possible that there is a significant amount of natural variation in leopard populations, such that drawing conclusions about the species as a whole is difficult. Additionally, studies have found social rank and sex to influence vigilance rates in chacma baboons as well as gelada monkeys (*Theropithecus gelada*) and mandrills (*Mandrillus sphinx*) (Johnson 2001; Cowlishaw 1998; Emory 1976). For example, Cowlishaw (1998) found that female baboons scanned for predators more frequently than males. Furthermore, it is possible that the results would be more accurate if I had defined 'scanning' more clearly than "looking back and forth in a horizontal plane." Although this type of vigilance has historically been associated with predator detection, there is no way to be sure whether or not this is the baboon's only intent. Pasternak (2011, p.24), for example, defined a specific category of "predator vigilance" as an individual that is "resting but alert, or interrupts another activity such as foraging to scan the environment to look at something other than vegetation and conspecifics." Other limitations include subjectivity in habitat classification during both behavioral data collection and GIS analysis. Finally, it is possible that the presence of an observer could have influenced baboon and leopard behavior. Baboons could

potentially exhibit different scanning rates when near a researcher, using humans as a kind of anti-predator 'shield' (Nowak *et al.* 2014). Furthermore, leopards could be more hesitant to attempt an attack if observers are standing among the troop – Lynne Isbell and Truman Young (1994) found that leopards predated upon vervet monkeys more often when researchers were absent than when they were at the field site.

Conclusions

Overall, baboons' behavior aligned moderately well with the 'actual' threat posed by leopards at the study site. Baboons showed a preference for rocky habitats and leopards for dense ones, and proximity events primarily occurred in habitats of intermediate vegetation density. Baboons exhibited lower scanning rates than expected in bush and grassland habitats. Scanning and social behavior was more frequent in high-use than low-use leopard areas, and baboons foraged less in intensely used leopard areas. Following a proximity event, the troop did not alter its group spread, but the baboons did increase their activity, perhaps as a means of escape. These findings support the idea that, although baboon behavior at this site might be fairly adaptive regarding anti-predator strategies, baboons may not have a wholly accurate perception of the risks they face.

Recommendations

As the protection of leopards outside of protected areas is of the utmost importance for their conservation in South Africa, it is important to study leopards at sites such as Lajuma (Chase Grey *et al.* 2013; Chase Grey 2010). Both leopards and baboons are increasingly threatened by habitat conversion and fragmentation as well as persecution (Chase Grey 2010).

Leopards in particular have lost over 35% of their historic range in Africa, and South Africa is one of the areas that has experienced the most marked declines (Henschel 2008). The main factor driving this decline is human-wildlife conflict, manifested in trophy hunting, bushmeat poaching, and illegal killing both for leopard parts and in retaliation for depredation of livestock (Panthera 2015). Although leopards have proven somewhat tolerant of habitat conversion and fragmentation due to their adaptable nature, they will only persist in such conditions if these threats are addressed and if they retain sufficient cover and prey availability (Henschel 2008). Thus, it is vital to understand factors such as habitat preference and predator-prey dynamics for leopards to be effectively protected. This study addresses these considerations, giving insight as to which areas leopards and baboons use most intensively and, thus, on which areas conservation efforts should be focused. Such concerns are particularly timely, as leopards' status on the International Union for the Conservation of Nature's (IUCN) Red List is expected to change from "Near Threatened" to "Vulnerable" in 2016 (Panthera 2015).

There are many ways the data in this study could be explored more thoroughly. For example, diurnal and nocturnal proximity events could be considered separately, alarm calling could be considered in addition to vigilance, and temporal variation in range use could be considered in addition to spatial variation. Furthermore, more comprehensive future studies on primate-predator interactions in the Soutpansberg should incorporate factors such as resource availability, seasonality, and multiple predator species for a more complete understanding of the factors affecting leopard and baboon movement in this area.

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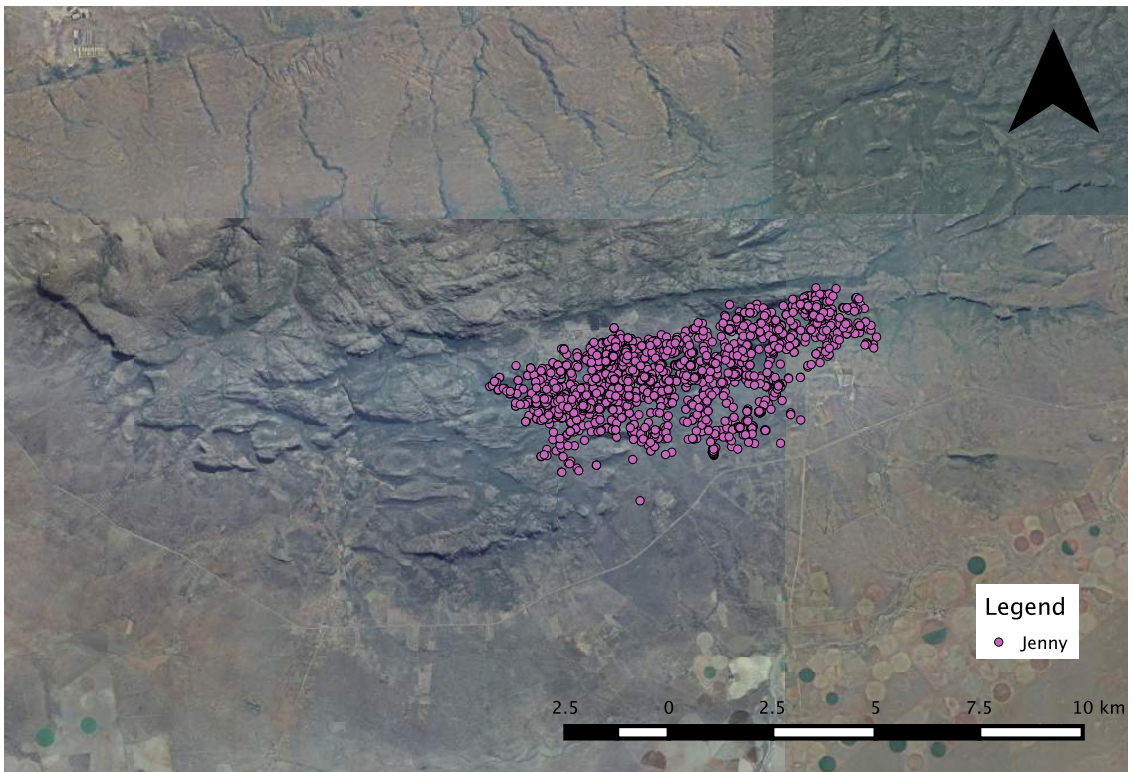
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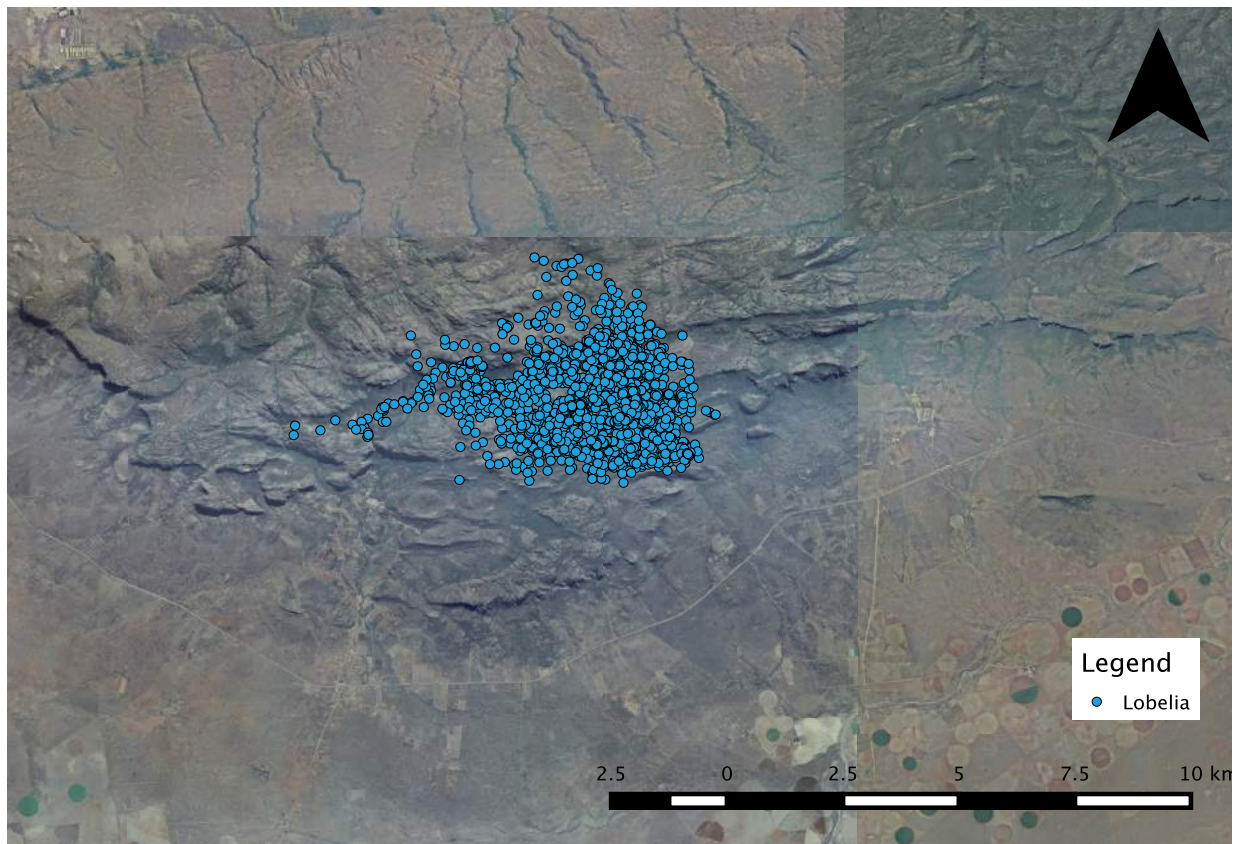
Figure 12. Lobelia's range. Data are from a GPS-collared baboon at Lajuma Research Centre in South Africa's Limpopo Province from between March 2013 and February 2014.
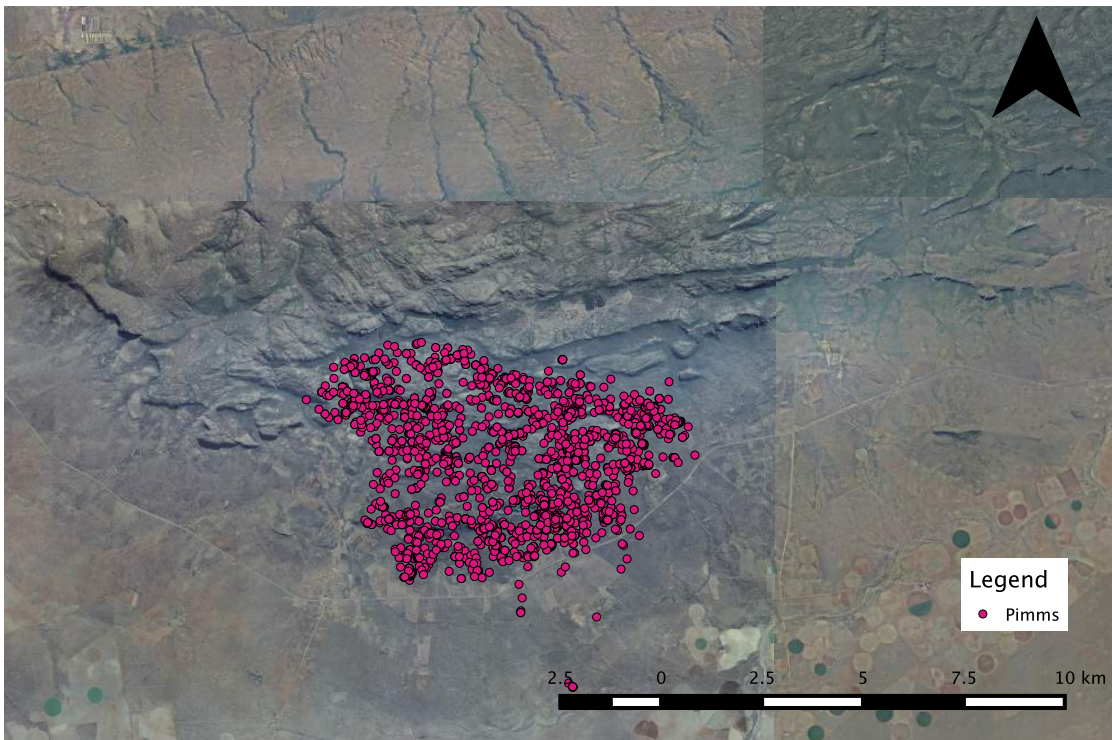
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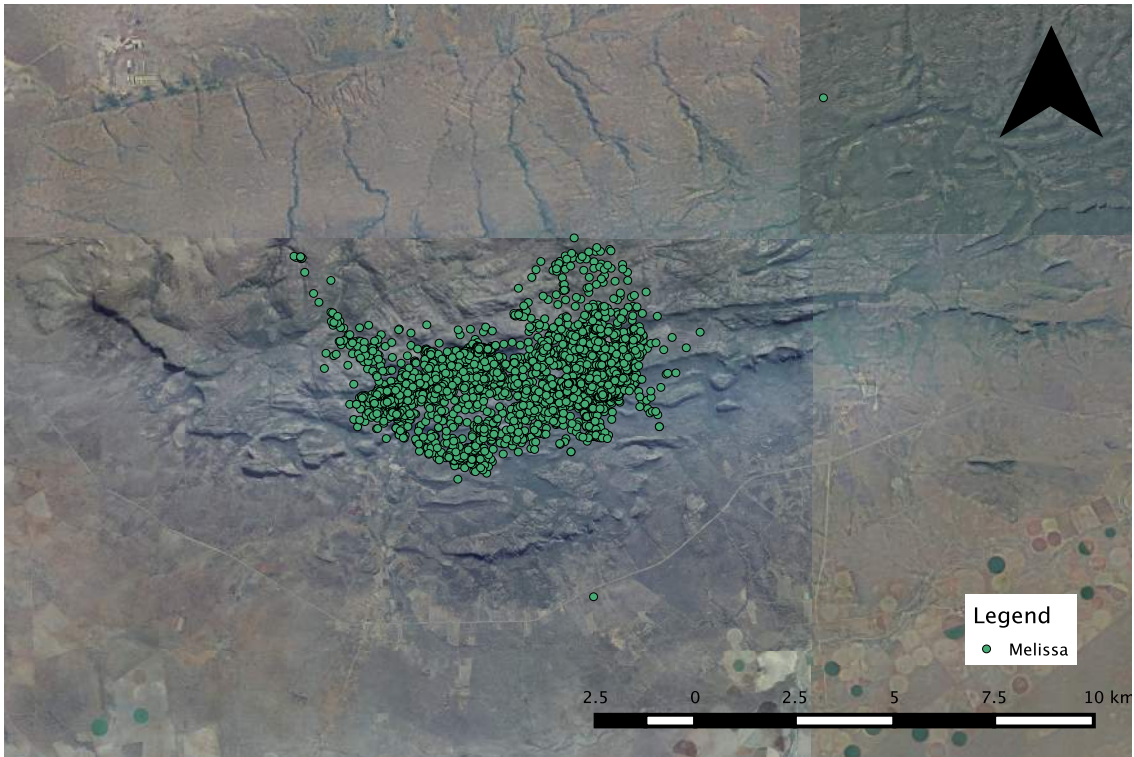
Figure 13. Melissa's range. Data are from a GPS-collared baboon at Lajuma Research Centre in South Africa's Limpopo Province from between July 2014 and August 2015.

Figure 14. Jenny's range. Data are from a GPS-collared leopard at Lajuma Research Centre in South Africa's Limpopo Province from between September 2013 and August 2014.

Figure 15. Pimms' range. Data are from a GPS-collared leopard at Lajuma Research Centre in South Africa's Limpopo Province from between July 2014 and June 2015.
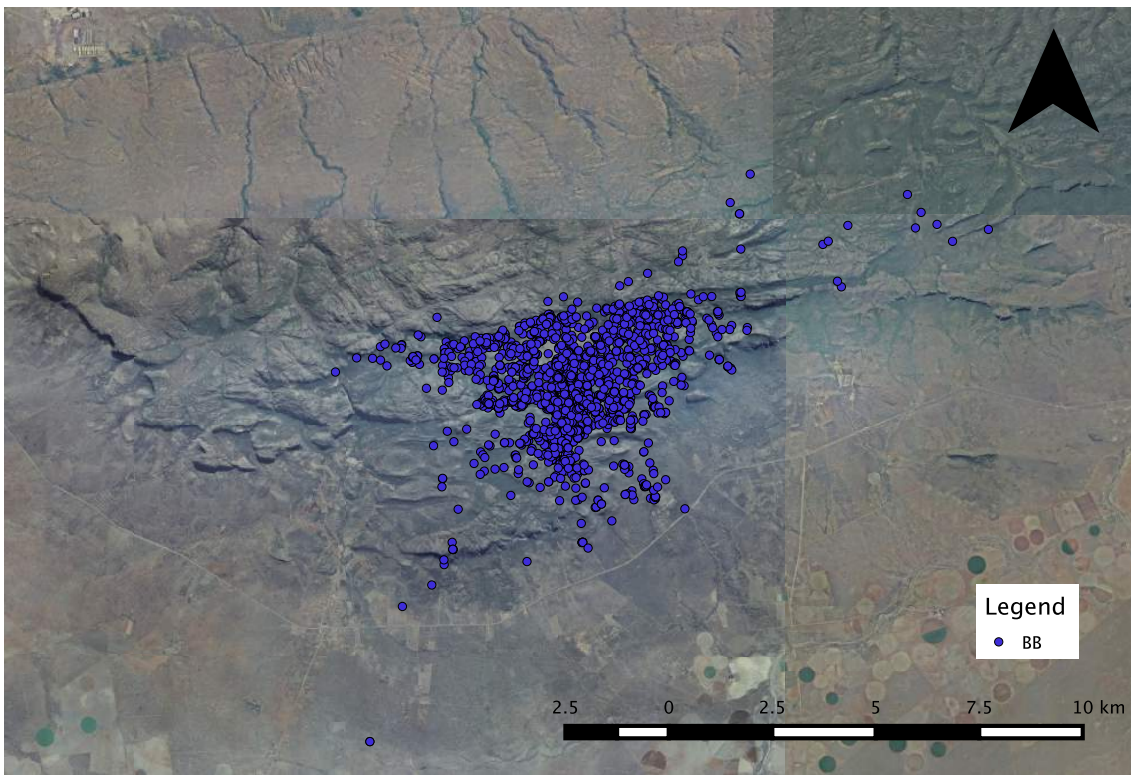

Figure 16. BB's range. Data are from a GPS-collared leopard at Lajuma Research Centre in South Africa's Limpopo Province from between June 2013 and March 2014.

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