



## GPS-identified vulnerabilities of savannah-woodland primates to leopard predation and their implications for early hominins

Lynne A. Isbell <sup>a, b, c, \*</sup>, Laura R. Bidner <sup>a, c</sup>, Eric K. Van Cleave <sup>b</sup>, Akiko Matsumoto-Oda <sup>c, d</sup>, Margaret C. Crofoot <sup>a, b, c, e</sup>

<sup>a</sup> Department of Anthropology, One Shields Ave., University of California, Davis, CA 95616, USA

<sup>b</sup> Animal Behavior Graduate Group, One Shields Ave., University of California, Davis, CA 95616, USA

<sup>c</sup> Mpala Research Centre, P.O. Box 555, Nanyuki, Kenya

<sup>d</sup> Graduate School of Tourism Sciences, University of the Ryukyus, Okinawa, Japan

<sup>e</sup> Smithsonian Tropical Research Institute, Balboa, Ancon, Panama

### ARTICLE INFO

#### Article history:

Received 4 November 2017

Accepted 8 February 2018

#### Keywords:

Predator-prey interactions

Antipredator behavior

Cercopithecin primates

Hominin behavior

### ABSTRACT

Predation is thought to have been a key selection pressure in primate evolution, especially in the savannah-woodland habitats where several early hominin species lived. However, predator-primate prey relationships are still poorly understood because human presence often deters predators, limiting our ability to quantify the impact of predation. Synchronized high-resolution tracking of leopards (*Panthera pardus*), vervets (*Chlorocebus pygerythrus*), and olive baboons (*Papio anubis*) during a 14-month study in Kenya revealed that increased vulnerability to leopard predation was not associated with higher encounter rates, smaller body size, smaller group size, or greater distance from refuges, contrary to long-standing inferences. Instead, the initiation, rate, timing, and duration of encounters, outcome of approaches, and predation events showed only a diel pattern of differential vulnerability. In the absence of human observers, vervets were more vulnerable during the day, whereas baboons were more vulnerable at night, but overall neither species was more vulnerable than the other. As our results show that leopards avoided baboons during the day and hunted them at night, we suggest that the same pattern would have applied to hominins—because they were even larger than baboons and bipedal, resulting in similarly offensive capability on the ground during the day but poorer agility in the trees at night, especially as they became committed bipeds. Drawing from hominid behavior and archaeopaleontological and ethnographic evidence, we hypothesize that ground-sleeping hominins initially dealt with this formidable threat by using stone tools to modify *Acacia* branches into ‘bomas’, thorny enclosures that provided nighttime shelter. The ability of hominins to create their own nightly refuges on the ground wherever *Acacia* spp. were available would have allowed them to range more widely, a crucial step in furthering the spread of hominins across Africa and beyond.

© 2018 Elsevier Ltd. All rights reserved.

### 1. Introduction

Since the 1960s, when field studies of primates began in earnest, predation has been viewed as a strong selection pressure affecting primate evolution, spurring morphological, cognitive, and social antipredator adaptations in the order (DeVore and Washburn, 1963; Crook and Gartlan, 1966; Dunbar, 1988; Willems and van Schaik, 2017), including early hominins as they expanded out of

African forests into mosaic savannah-woodland environments (Reed, 1997) where predation has long been considered especially intense (Crook and Gartlan, 1966; Dunbar, 1988). Non-human primates that live in such semiarid environments today have long served as models for reconstructing the behavior of these extinct hominins (DeVore and Washburn, 1963; Crook and Gartlan, 1966; Dunbar, 1988; Isbell et al., 1998; Elton, 2007; Bettridge and Dunbar, 2012; Strum, 2012; Willems and van Schaik, 2017). Two model primate species, vervet monkeys (*Chlorocebus pygerythrus*) and olive baboons (*Papio anubis*), live in multimale, multifemale groups and often occur sympatrically in semiarid savannah-woodlands of sub-Saharan Africa (Melnick and Pearl, 1987).

\* Corresponding author.

E-mail address: [laisbell@ucdavis.edu](mailto:laisbell@ucdavis.edu) (L.A. Isbell).

Although baboons are substantially larger than vervets and live in larger groups—traits that are argued to have evolved in response to predators (Crook and Gartlan, 1966; Clutton-Brock and Harvey, 1977; van Schaik, 1983; Dunbar, 1988)—both remain vulnerable to predation, with leopards (*Panthera pardus*) being their main predators (Isbell, 1990; Cowlishaw, 1994; Cheney et al., 2004; Isbell et al., 2009). However, they typically constitute only a small percentage of the leopard's diet because leopards are eclectic predators (Hayward et al., 2006; Hunter et al., 2013). Leopards kill prey both larger and smaller than primates, including the 345 kg eland (*Tragelaphus oryx*) and the 0.5 kg meerkat (*Suricata suricatta*), while preferring prey between 10 and 40 kg, such as impala (*Aepyceros melampus*) and bushbuck (*Tragelaphus scriptus*; Hayward et al., 2006). A literature survey found that leopards are predators of at least 111 species, including 18 species of primates (Hayward et al., 2006). Leopards kill arboreal as well as terrestrial primates, and smaller primates such as guenons (*Cercopithecus* spp.), to the largest primates, gorillas (*Gorilla gorilla*) and humans (*Homo sapiens*; Schaller, 1963; Fay et al., 1995; Hart et al., 1996; Treves and Naughton-Treves, 1999; Hayward et al., 2006; Hunter et al., 2013).

Along with larger body size and larger group size, other factors long thought to reduce predation on primates include lower encounter rates with predators and closer proximity to refuges such as cliffs and trees (Crook and Gartlan, 1996; Dunbar, 1988; Cowlishaw, 1997). All these assumptions are intuitively appealing and have persisted for years, but, as yet, little direct evidence exists to support them (Cheney and Wrangham, 1987; Isbell, 1994; Miller and Treves, 2007).

Quantifying the impact of predation on primates and testing hypotheses about predation as an important selection pressure have proven difficult because the standard observational approach used to study primates in the field, i.e., following them on foot, can also deter potential predators. Because leopards are shy and avoid humans (Bailey, 1993; Ngoprasert et al., 2007), including researchers studying predator-prey dynamics (Isbell and Young, 1993), direct observations of leopard predation are rare. In a decade-long study of chacma baboons (*Papio ursinus*) in Botswana, only three attacks were ever witnessed (Cheney et al., 2004). In a 26-month study of vervets in southern Kenya, no attacks were witnessed and remains were found of only one individual even though indirect evidence suggested leopard predation was particularly severe for six of those months (Isbell, 1990). Similarly, during an 11-year study of vervets in central Kenya, leopard predation was strongly implicated in the rapid decimation of two study groups, but no attacks were ever witnessed and remains were found of only five individuals (Isbell et al., 2009).

We overcame the logistical problem of observer interference with predator behavior by using Global Positioning System (GPS) tracking and triaxial accelerometers to collect data on interactions between leopards and their primate prey, in order to better understand the dynamics of predator-prey interactions in this important model system. This is the first study to synchronously track the movements of leopards and their primate prey on a fine temporal scale, an approach that affords the opportunity to quantitatively test for the first time some of the most enduring hypotheses about the role of predation on primates.

Because the study was conducted in an East African savannah-woodland habitat similar to the environments where the genus *Homo* is thought to have evolved (Reed, 1997), our findings also inform our understanding of the vulnerability of early hominins to leopards and allow us to suggest possible reconstructions of hominin antipredator behavior. Hominins would have encountered leopards or leopard-like felids (hereafter, leopards) beginning from about 3.5 to 2.0 Ma, when the ancestors of modern leopards are first recorded in Africa (Turner, 1990; Turner and Anton, 1997;

Uphyrkina et al., 2001; Werdelin and Lewis, 2005). At 28–52 kg, hominins living then were within or close to the preferred prey size range of modern leopards (McHenry, 1991, 1992, 1994; Bailey, 1993; Hayward et al., 2006; Hunter et al., 2013), and evidence that leopards preyed on hominins comes from the *Paranthropus robustus* SK 54 juvenile hominin's partial cranium (Brain, 1970, 1981) as well as taphonomic and stable isotope analyses at Swartkrans (Lee-Thorp et al., 2000; Pickering et al., 2008). Baboon fossils have also been found at Swartkrans, and many also appear to have been deposited as a result of leopard predation (Brain, 1981, 1993; Sillen and Lee-Thorp, 1994; Pickering et al., 2008). Despite the persistent danger from leopards that primates have experienced over evolutionary time, we currently lack basic information on leopard-primate interactions to reconstruct leopard-hominin interactions with confidence.

We had six specific goals guiding our research. We sought to 1) understand how leopards move in relation to baboons and vervets, and vice versa; 2) obtain an estimate of encounter rates between leopards and the two primate species; 3) determine the vulnerabilities of the two primate species; 4) document predation events by leopards and estimate predation rates for the two primate species; 5) test a core hypothesis of socioecology that smaller body size and smaller group size increase vulnerability to predators; and 6) apply our findings to further understand how early hominins might have dealt with leopards. In this context, we offer a) a novel hypothesis that ground-sleeping hominins, i.e., early members of *Homo* that were fully committed to bipedalism, reduced nighttime predation by building and sleeping within thorny *Acacia* enclosures, or 'bomas', b) propose a possible test of the hypothesis, and c) suggest possible consequences of such a strategy on hominin movements. Throughout we take a comparative perspective to more fully understand how multiple primate species have managed to co-occur with the same predator for several million years.

## 2. Materials and methods

### 2.1. Study site and subjects

We conducted a 14-month field study from December 2013 to January 2015 in the semiarid bushlands and riverine woodlands around Mpala Research Centre (MRC) on the Laikipia Plateau of central Kenya (0.29° N, 36.90° E; rainfall in 2014 = 443.2 mm). Mpala is a working cattle ranch and wildlife conservancy with a nearly intact mammalian community; at least 14 species of ungulates and six species of large carnivores inhabit the area (Young et al., 1998).

We trapped one subadult male and three adult female leopards with foot snares (Frank et al., 2003), immobilizing them with ketamine and medetomidine, and later reversing the drugs with atipamezole. While they were immobilized, we fitted them with GPS collars ranging from 495 to 607 g (2.0–2.2% of body mass; Savannah Tracking, Inc., Nairobi, Kenya). We used modified box traps (Grobler and Turner, 2010) to capture 12 adult female vervets in five groups (at least two/group), and wire cage traps (Jolly et al., 2003) to capture six adult female baboons in four groups. We immobilized them with ketamine and fitted vervets with GPS collars ranging from 146 to 151 g (4.4–6.0% of body mass) and baboons, with GPS collars ranging from 452 to 468 g (2.9–4.9% of body mass; Table 1).

Since vervets and baboons live in cohesive groups, the locations of the collared primates were considered representative of the locations of their groups except on four occasions. Three occasions involving vervets were clearly GPS errors and were excluded from analyses. They were identified by coordinate locations that

**Table 1**  
Group sizes and characteristics of animals trapped and collared.

Species	Individual	Body mass (kg) <sup>a</sup>	Group ID	Group size	
Vervet	GS <sup>b</sup>	–	CT	4–7 <sup>e</sup>	
	AS <sup>c</sup>	2.5	CT		
	CO	2.3	CT		
	GG	3.0	BR	15 <sup>f</sup>	
	TZ	2.8	BR		
	ME	3.4	KU	21 <sup>g</sup>	
	MK <sup>c</sup>	2.7	KU		
	CD <sup>c</sup>	3.9	HP	30–35 <sup>e</sup>	
	CV <sup>b</sup>	2.8	HP		
	PI	3.0	HP		
	BU	3.4	FG	22 <sup>f</sup>	
	KA	3.5	FG		
	Olive baboon	YK	–	AI	58–63 <sup>e</sup>
		WG	12.3	AI	
TH <sup>c</sup>		15.9	LI	59 <sup>h</sup>	
LU <sup>b</sup>		11.0	LI		
MS		11.4	ST	56–65 <sup>i</sup>	
SH		14.0	MG	43–49 <sup>i</sup>	
Leopard	KO (AF) <sup>d</sup>	25.5			
	HA (AF)	24.0			
	CH (AF)	27.3			
	TA (SAM) <sup>d</sup>	33.6			

<sup>a</sup> All body masses recorded at the beginning of the study except for CO, whose body mass was recorded at the end of the study.

<sup>b</sup> Died of unknown causes.

<sup>c</sup> Died of leopard predation.

<sup>d</sup> AF = adult female; SAM = subadult male.

<sup>e</sup> Regular censuses of known individuals.

<sup>f</sup> Repeated counts at end of study.

<sup>g</sup> One complete count.

<sup>h</sup> Mean of 19 opportunistic counts.

<sup>i</sup> Estimated range based on one incomplete count.

indicated one of the two vervets within a group was well outside the group's home range and far away from her coordinate locations 15 min before and after the outlier. The fourth occasion occurred during one 7-day period, when two collared baboons from the same group became separated. The mean distance between them before that week was  $52 \text{ m} \pm 0.79 \text{ SE}$  ( $n = 12718$ ), and during that week,  $2919 \text{ m} \pm 53.8 \text{ SE}$  ( $n = 598$ ).

We avoided approaching on foot all but three groups to minimize the potential for human interference in leopard movements. One vervet group (CT) already lived near humans at the main campus of MRC, another vervet group (HP) spent much of its time at a sleeping site where we censused them nearly every morning (Isbell and Bidner, 2016), and one baboon group (AI) was the focus of a concurrent behavioral study during which it was observed on foot nearly every morning and evening at its primary sleeping site. The other six groups were exposed to humans mainly through occasional vehicular traffic and herders on foot. Group sizes were obtained by regular censuses of known individuals (in study groups CT, HP, and AI), estimates from opportunistic counts throughout the study, or by complete group counts at the study's end during trapping to remove collars (Table 1).

## 2.2. Data collection and analyses

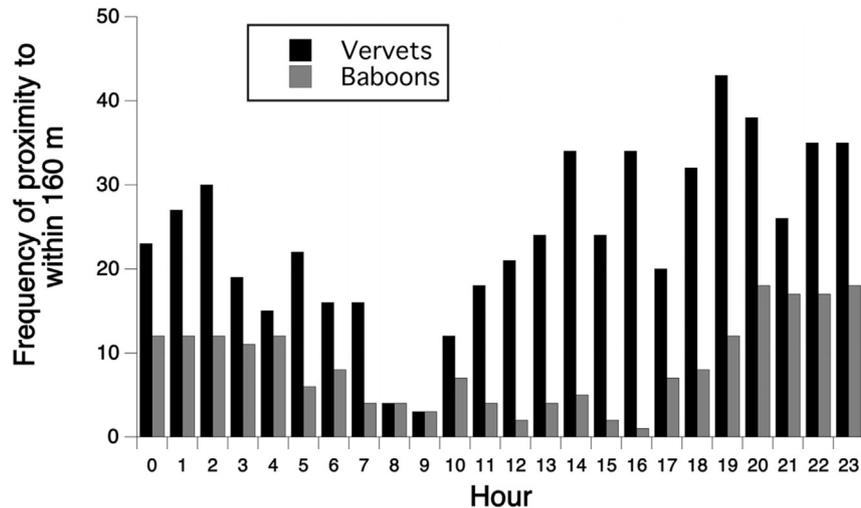
All collars were programmed to take GPS data every 15 min, and triaxial accelerometer data for 3 s/min at 32 Hz, synchronously and continuously throughout the lives of the collars. We used a base station (e-obs GmbH, Gruenwald, Germany) and an omnidirectional marine antenna (cxl 900-3LW: Procom, Frederikssund, Denmark), and also for the leopards, a nine-element Yagi antenna (YAGI-869A: Low Power Radio Solutions, Witney, United Kingdom) to download GPS and accelerometer data remotely when within UHF range of each collar. We tested the accuracy of the collars by

examining 1122 readings from two stationary collars. The mean difference in distance between readings was  $11 \text{ m} \pm 20 \text{ SD}$  ( $n = 275$ ), and  $12 \text{ m} \pm 10 \text{ SD}$  ( $n = 847$ ). The GPS units attempted 65,420 location fixes for the four leopards with an overall 97.2% success rate (range among individuals = 95.6–98.1%), 160,310 for the six baboons (overall success rate = 96.5%, range = 90.6–98.6%), and 303,984 for the 12 vervets (overall success rate = 99.1%, range = 98.0–99.4%). The lifespans of the collars ranged from 3 to 14 months. Two leopard collars failed after three months and were replaced within three months with collars that lasted until the end of the study. Two other leopard collars failed after three months and were removed, but not replaced, because the subadult male leopard (TA) had begun to disperse and one female (CH) had little home range overlap with the primate groups. One baboon collar failed after 10 months and one vervet collar, after 12 months; all other primate collars continued transmitting until the end of the study or until the animals died prior to the end of the study. The GPS and accelerometer data are deposited in Movebank (Wikelski and Kays, 2017), an online repository for animal movement data.

We calculated home ranges and home range overlaps using the 'adehabitatHR' package for R (Calenge, 2006). For each leopard and primate group, we estimated utilization distributions (UD) using fixed kernel estimations. UD are probability density functions estimated from location observations that describe the relative use at a given location by individuals or groups (Kernohan et al., 2001). We determined home ranges from these UD by defining a home range as the contour boundary encompassing 99% of the UD density. We calculated the extent of home range overlap between each dyad (consisting of all combinations of individual leopards and primate groups) as the percentage of the home range of one member of the dyad that was shared with the other member of the dyad.

To estimate proximity between leopards and primates at each 15-min sample, we imported all GPS data into a Microsoft Excel spreadsheet and calculated the difference in meters (D) between each set of paired coordinates for each leopard-primate dyad using the equation  $D = 110365 \cdot \sqrt{((A_{lo} - B_{lo})^2 + (A_{la} - B_{la})^2)}$ , where 110365 is in m/degree, A = Animal A, B = Animal B, lo = longitude, and la = latitude. For analyses, we extracted all spatial data in which leopards and primates were within 160 m of each other and for two 15-min samples before and after proximity to 160 m. In the absence of any a priori estimate for the maximum distance at which leopards and primates may interact, we used 160 m as the cutoff distance based on the mean of group spreads taken every 30 min while censusing the largest vervet group (mean =  $160 \text{ m} \pm 35 \text{ m SD}$ ,  $n = 399$ ). Although comparable estimates of group spread were not available for baboons, the mean group diameter per second over 14 days for one baboon group (MG) in which most adults were collared for an earlier study was  $58.9 \text{ m} \pm 37.6 \text{ m SD}$  perpendicular and  $67.8 \text{ m} \pm 45.1 \text{ m SD}$  parallel to the direction of travel (Crofoot et al., 2015), well within our measure of proximity. Mean distances between collared vervet dyads within groups (range =  $22.6\text{--}82.6 \text{ m} \pm 38.27\text{--}81.39 \text{ m SD}$ ,  $n = 4187\text{--}34386$ ) and between collared baboon dyads within groups (range =  $40.2\text{--}51.7 \text{ m} \pm 59.8\text{--}88.2 \text{ m SD}$ ,  $n = 12713\text{--}22102$ ), excluding the 7-day separation of two female baboons, also accord well. We confirmed that both vervets and baboons can see leopards during the day, at least in the open, at a distance of 160 m by noting alarm calls given when we placed a life-sized, two-dimensional leopard model (Stankowich and Coss, 2007: Fig. 1b) 163 m from them. The 160 m cutoff distance is likely conservative; collared leopards began their approaches to the collared primates they killed well before they were within 160 m of the primates (see Results).

When we had more than one collared individual in a primate group, to avoid double-counting encounters we used the data from



**Figure 1.** Hourly distributions of all 15-min GPS point samples when leopards were within 160 m of focal vervet and baboon groups ( $n = 571$  and  $206$ , respectively).

the individual that had the fewest interrupted fixes and was closest to the leopard during the encounter. Encounters were considered independent events if they were separated by at least 60 min during which the dyad was beyond 160 m, and were categorized as occurring either during the day (06:45–18:45) or night (19:00–06:30). We excluded encounters that could not be classified as occurring predominantly in either time period. These events were few, occurring in, for vervets, 0.7% ( $n = 5$ ), and for baboons, 0.01% ( $n = 1$ ) of 688 leopard-primate 24 h (diel) periods. For analyses involving days vs. nights, encounters by the same leopard with more than one primate group at the same time were scored as separate events, as were encounters by two leopards with one group.

Encounter rates were likely affected by the extent of home range overlap between individual leopards and primate groups and so could not be compared directly. To control for variation in home range overlap, we calculated standardized encounter rates by using the frequency of encounters per total number of functional collar-hours per leopard, since their collars had shorter lifespans than the primate collars, multiplied by the proportion of each primate group's home range that was included in each leopard's home range.

We used relative movements of leopards and primates to operationally define behavior during encounters (approaches to within 160 m), as well as departures (moving beyond 160 m), lingering before leaving (at least two GPS fixes within 160 m), passing by (only one GPS fix within 160 m), and remaining in place (staying while the other species left). We calculated speeds of movement per min from the difference between consecutive GPS locations. Visualization of encounters and movement directions was conducted using Google Earth Pro v. 7.1.5.1557.

We used the Brown index (Brown, 2001) to identify the extent to which leopards were responsible for changes in proximity during encounters

$$100 \left( \frac{Al + Ll}{Al + Ll + Ap + Lp} \right)$$

where Al is the number of times leopards approached primates, Ll is the number of times leopards left primates, Ap is the number of times primates approached leopards, and Lp is the number of times primates left leopards. Higher values indicate greater responsibility for changes in proximity by leopards. We excluded mutual approaches and leaves.

We also tested for attraction and avoidance among leopard-primate dyads using MoveMine, an online software program for mining movement databases (Li et al., 2013; <https://faculty.ist.psu.edu/jessiel/MoveMine/>). In these analyses, observed encounter rates between dyads, defined by a distance threshold  $D$  (in our case, 160 m), are compared to the number of encounters that would be expected to occur if animals moved independently through their home ranges. The distribution of expected encounter rates under the null model of independent movement is generated for each dyad by repeatedly permuting the GPS fixes in the movement sequence of one animal (i.e., randomly shuffling the timestamps associated with each location). The statistical significance of the observed number of encounters (whether greater or less than expected by chance) is obtained by comparing the observed number to the tails of the null distribution. We ran 1000 permutations each for day and night.

We classified leopard predation as confirmed or suspected when we had simultaneous GPS trackings showing convergence of leopard and primate locations with subsequent retrieval of the primate's collar, a photograph of a leopard with a primate in its mouth, physical remains along with a leopard sighted nearby, or intact GPS collars and primate remains (bone shards and fur along with mandible or maxilla) in locations consistent with leopard feeding behavior, e.g., under bushes or in thick vegetation near or in luggas (dry streambeds). Predation rates were calculated using the total number of diel periods (or, for day and night only, 12-h periods) in which leopards were within 160 m of primate groups at least once. Population sizes were based on known group sizes and midpoints for estimated group sizes. We conducted descriptive statistical analyses using VassarStats (Lowry, 1998). Unless specified otherwise, the standard error of the mean was the measure of error and tests were two-tailed.

### 3. Results

#### 3.1. Home ranges and encounter rates

Substantial but also variable overlap existed between the home ranges of our primate study groups and collared individual leopards. Vervet group home ranges were 0–100% within each of the four leopard home ranges, and baboon groups, 0–50% (Table 2). During 688 collared leopard-primate diel periods, leopards had 142 encounters with vervet study groups and only 49 encounters with baboon study groups. The hourly distributions of all leopard

locations within 160 m of vervets and baboons are shown in Figure 1. Controlling for variation in home range overlap, encounter rates with leopards were significantly higher for vervets than for baboons (mean ranges per leopard = 1.3–7.7 encounters per 100 diel periods vs. 0.09–1.7 encounters per 100 diel periods, respectively; t-test:  $t = 3.0$ ,  $p = 0.02$ ,  $n = 8$ ,  $df = 6$ ). Encounter rates between leopards and vervets were higher during the day than at night (mean ranges per leopard: day = 1.3–4.7 encounters per 100 days, night = 0–3.3 encounters per 100 nights; paired t-test:  $t = 2.84$ ,  $p = 0.03$ ,  $n = 4$ ,  $df = 3$ , one-tailed), whereas encounter rates between leopards and baboons were distributed more evenly between day and night (mean ranges per leopard: day = 0.1–0.78 encounters per 100 days, night = 0–0.89 encounters per 100 nights; paired t-test:  $t = 0.25$ ,  $p = 0.41$ ,  $n = 4$ ,  $df = 3$ , one-tailed).

### 3.2. Durations of proximity

Leopards and vervets stayed near each other for a mean of 3.2 consecutive GPS readings  $\pm 0.34$  SE (~35–45 min) whenever they were within 160 m (periods with consecutive readings,  $n = 179$ ). Durations did not differ significantly between night and day (means: night = 3.5 GPS readings  $\pm 0.61$ ,  $n = 93$ ; day = 2.9 GPS readings  $\pm 0.28$ ,  $n = 86$ ; t-test:  $t = -0.84$ ,  $p = 0.40$ ,  $df = 177$ ). Leopards and baboons stayed near each other for a mean of 4.9 consecutive GPS readings  $\pm 1.18$  (~60–75 min) whenever they were within 160 m ( $n = 51$ ). Durations were significantly longer at night than during the day (means: night = 9.6 GPS readings  $\pm 2.66$ , ~140–160 min,  $n = 20$ ; day = 1.8 GPS readings  $\pm 0.27$ , ~10–25 min,  $n = 31$ ; t-test:  $t = -3.65$ ,  $p = 0.0006$ ,  $df = 49$ ).

### 3.3. Initiators of encounters

Leopards were responsible for initiating and ending most encounters with vervets, both during the day and at night, as indicated by Brown index values of 64 and 98, respectively. Similarly, and as expected, leopards were responsible for all the changes in proximity to baboons at night (Brown index = 100), but unexpectedly, they were responsible for very few such changes during the day (Brown index = 10).

### 3.4. Leopard movements and behavior during encounters

Leopards who approached and lingered (stayed within 160 m for at least two GPS fixes) near vervets moved at a mean speed of 3.1 m/min  $\pm 0.37$  ( $n = 46$ ). Leopards who passed by vervets (only

one GPS fix within 160 m) moved five times faster (mean = 15.1 m/min  $\pm 0.91$ ,  $n = 58$ ). Leopards lingered near vervets more often during the day ( $n = 25$ ) and passed by them more often at night ( $n = 40$ ;  $\chi^2 = 4.83$ ,  $p = 0.03$ ,  $df = 1$ ). Greater lingering during the day suggests that leopards were more motivated to hunt vervets then, and, indeed, all three confirmed or suspected kills of vervets by leopards occurred in treeless bushlands or an open glade near trees during the day (Fig. 2).

Leopards approached vervet groups in a highly directed manner more often at night than during the day (46 of 60 [77%] nighttime encounters; 21 of 43 [49%] daytime encounters;  $\chi^2 = 7.35$ ,  $p = 0.007$ ,  $df = 1$ ). However, leopards also moved along the river more often at night (23 of 56 [41%] nights vs. 4 of 40 [10%] days, respectively;  $\chi^2 = 9.66$ ,  $p = 0.001$ ,  $df = 1$ ). Because leopards were more likely to pass by than linger near vervets at night, their directed movement toward vervets is more likely due to a topographical constraint on movement imposed by the river, where vervets generally sleep, than an indication of motivation to hunt vervets.

Baboon sleeping sites occurred on kopjes (rock outcroppings), as well as along the river, and leopards were presumably less constrained by topography when they approached baboons at night. Indeed, they moved more often through the bush (14 of 16 [88%] nights) than along the river ( $\chi^2 = 7.56$ ,  $p = 0.006$ ,  $df = 1$ ) when they approached baboons at night. On 57% (8/14) of the nights when leopards moved through the bush toward baboons, they moved directly to them at their sleeping sites, indicating an interest in hunting baboons on those nights. Of the four baboons that died of confirmed or suspected leopard predation during this study, three died at night and all died at their sleeping sites (Figs. 3 and 4).

Leopards remained in place more often than expected by chance when baboons approached them during the day (18 of 21 [86%] events;  $\chi^2 = 9.34$ ,  $p = 0.002$ ,  $df = 1$ ). Baboons are known to attack and kill leopards (Cowlshaw, 1994; Cheney et al., 2004), and during this study we observed several adult male baboons chase an uncollared leopard away from bushes near their sleeping site during the day. Thus, it is likely that leopards were attempting to avoid being detected rather than lying in wait to ambush. No female leopards behaved as if they were interested in hunting baboons during the day, but the subadult male leopard twice followed baboon groups after they passed by.

### 3.5. Primate movements and detection of leopards

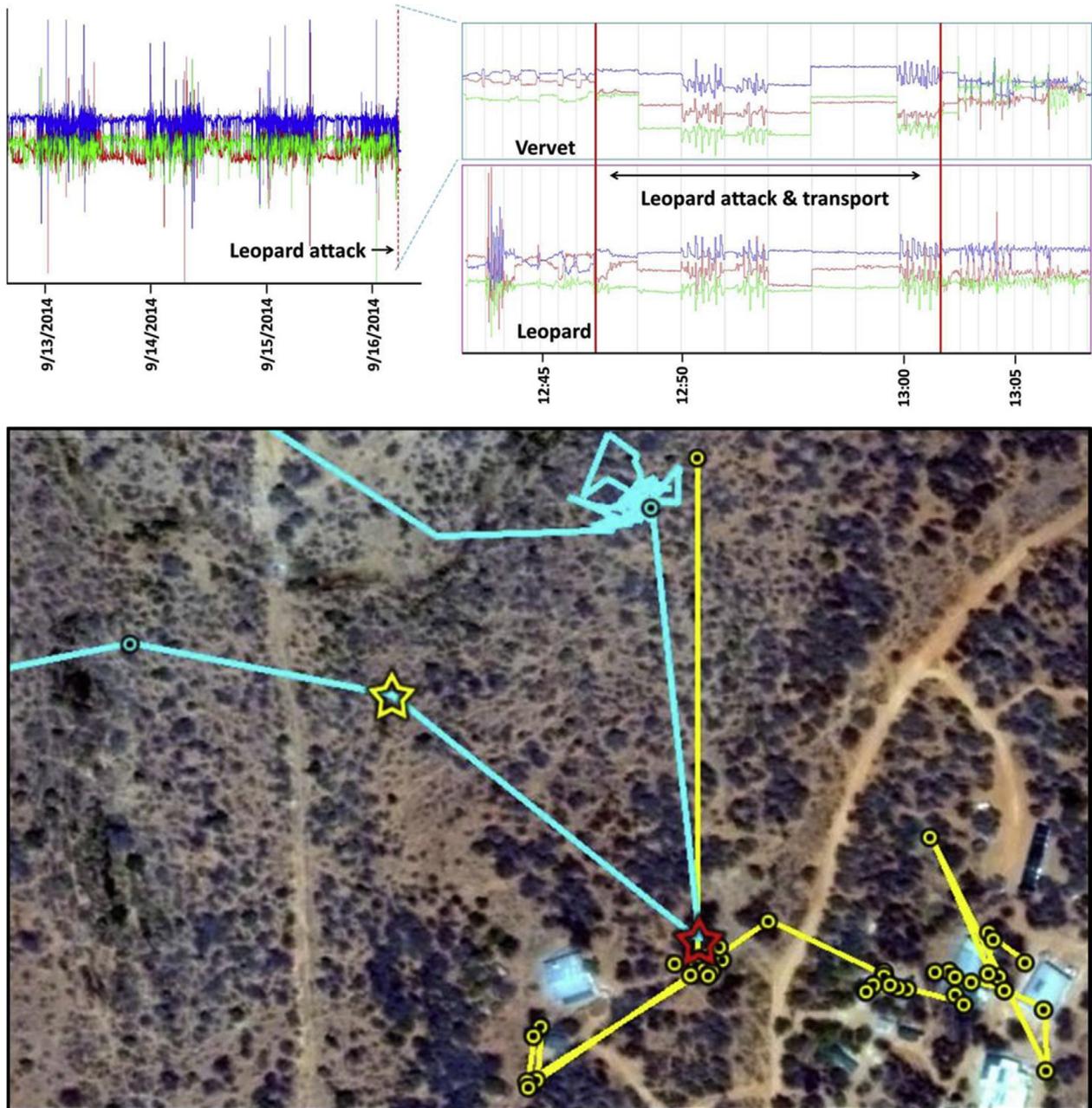
In 34% (23/67) of daytime encounters, either vervets moved toward leopards or the approaches were mutual, suggesting that vervets were initially unaware of leopards on at least one-third of all daytime encounters, since they do not approach detected leopards but flee to nearby trees and remain there (Cheney and Seyfarth, 1981). Larger groups are expected to detect predators earlier or more reliably than smaller groups because there are more individuals available to monitor the environment, but there was no correlation between vervet group size and the ratio of approaches to encounters ( $r = 0.32$ ,  $p > 0.60$ ,  $n = 5$ ,  $df = 3$ ; Fig. 5), nor was there a significant difference in daytime approaches/encounters between the smallest and largest vervet groups (7/26 vs. 6/17, respectively;  $\chi^2 = 0.34$ ,  $p = 0.56$ ,  $df = 1$ ).

When baboons approached leopards during the daytime, in 38% (8/21) of encounters they either veered off, curved around the leopard, or returned back the way they came, movements suggesting that they had detected the leopard and were avoiding it. More often (13 of 21 [62%] encounters), baboons maintained their travel direction and passed by, moving as if they were unaware of the leopard's presence then. On one occasion, after a mutual approach, baboons may have chased a collared leopard as

**Table 2**  
Extent of home range overlap between collared leopards and primate groups.<sup>a</sup>

IND.	Leopards				Vervets					Baboons			
	CH	KO	HA	TA	CT	BR	KU	HP	FG	LI	ST	AI	MG
CH		80	<1	30	<1	0	0	0	0	0	2	53	0
KO	50		15	44	<1	1	2	0	0	4	19	64	0
HA	<1	27		73	0	<1	3	2	3	26	38	64	6
TA	17	40	36		0	1	2	<1	2	42	47	60	14
CT	100	100	0	28		0	0	0	0	0	6	100	0
BR	0	100	39	100	0		34	0	0	0	86	100	0
KU	0	80	99	100	0	22		14	0	40	100	100	0
HP	0	1	100	100	0	0	30		0	100	100	100	0
FG	0	0	97	100	0	0	0	0		100	100	24	2
LI	0	4	14	44	0	0	<1	<1	2		60	20	38
ST	1	18	20	50	0	1	2	<1	2	60		36	6
AI	15	28	16	30	<1	<1	<1	<1	<1	90	17		2
MG	0	0	4	17	0	0	0	0	0	0	4		0

<sup>a</sup> Values are percentages of home ranges shared with a primate group or individual leopard, e.g., 80% of CH's home range was shared with KO. Individual leopards and primate groups are identified by two-letter code.



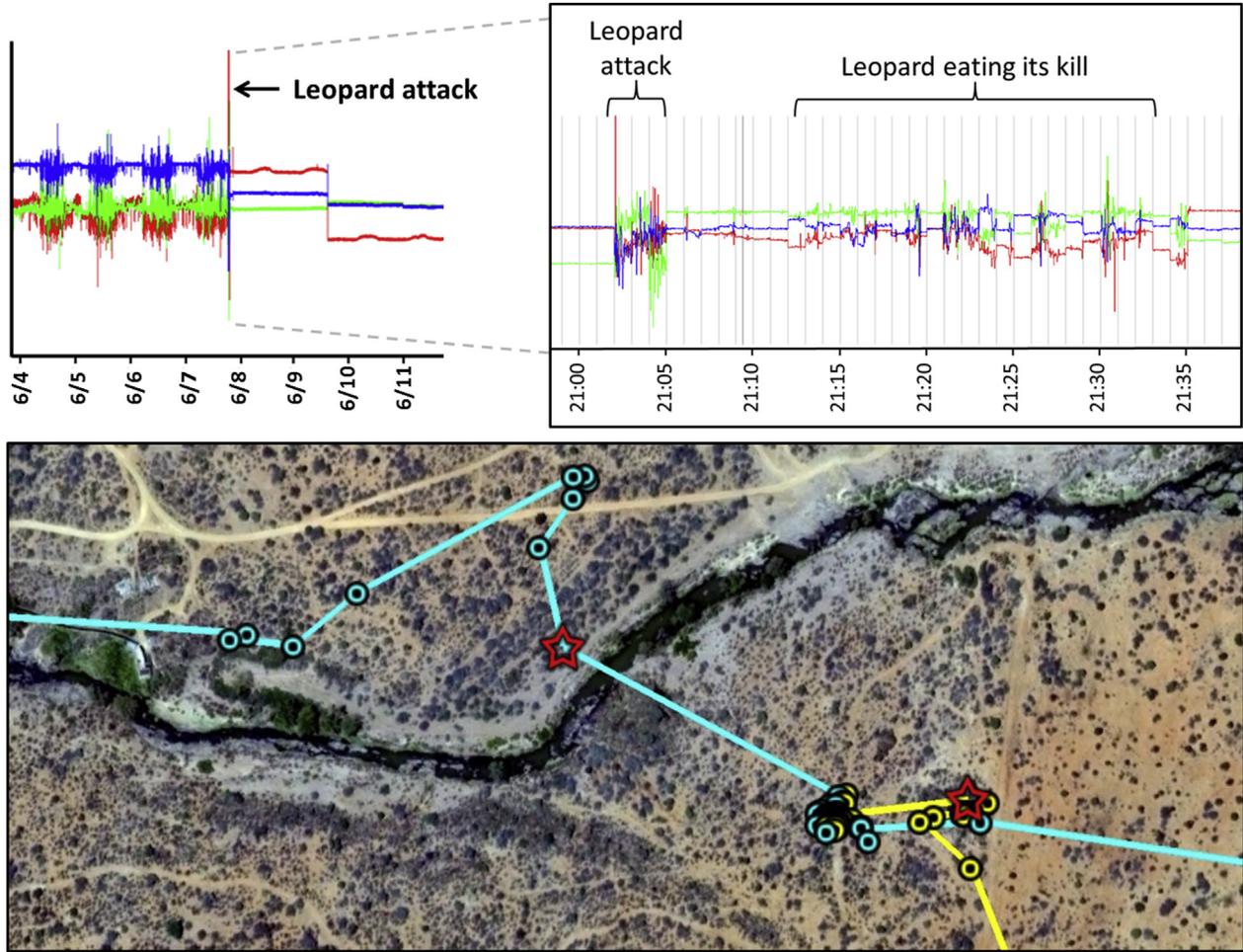
**Figure 2.** Predation on a collared vervet by a collared leopard. The vervet's 3D accelerations in the days before death (left) show consistent diurnal patterns of activity and become synchronized with the leopard's 3D activity patterns in the minutes before and after death (right), indicating attack and transport. GPS data (bottom) showing movements of the leopard and vervet before and after attack. The leopard (KO; aqua) began to move toward the vervet (AS; yellow) when they were 234 m apart. She then moved 144 m between 12:30 (yellow star) and 12:45 (9.6 m/min), to 9 m from the vervet. By 12:48 the leopard attacked (red star) and then carried the vervet 208 m before eating her. The leopard remained there for 15 h before moving >1 km away in 15 min. Aqua rectangles: Mpala Research Centre buildings.

evidenced by the leopard's rapid movement away from the collared baboons. We did not test for group-size effects on predator detection in baboons, because there were too few cases in which each group detected a leopard. Based on their movements when leopards were in proximity, baboons appeared to detect leopards less often than vervets did during the day ( $\chi^2 = 3.95$ ,  $p = 0.05$ ,  $df = 1$ ), even though their groups were larger.

### 3.6. Intraspecific variation in predator-prey relationships

Analysis of probabilities of proximity to 160 m revealed extensive individual and group variation in predator-prey

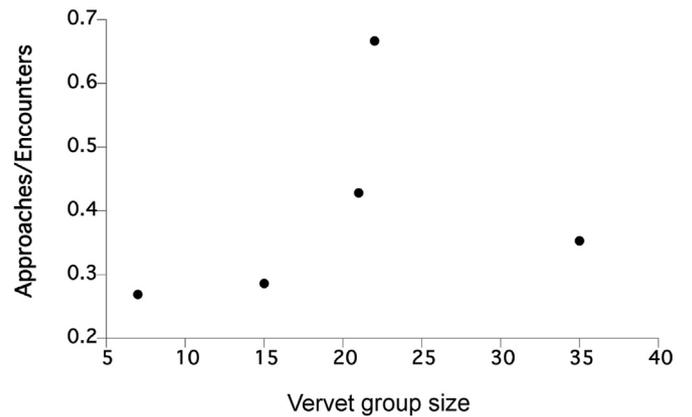
relationships (Fig. 6). Some of this can be explained by variation in degree of home range overlap between individual leopards and primate groups. However, we also note that the same leopard could have different relationships with different individuals in the same group. For example, leopard KO had attractant relationships with vervets AS and GS, but an avoidant relationship with their groupmate CO (Fig. 6), driven by changes in KO's movements in the months after AS and GS died.



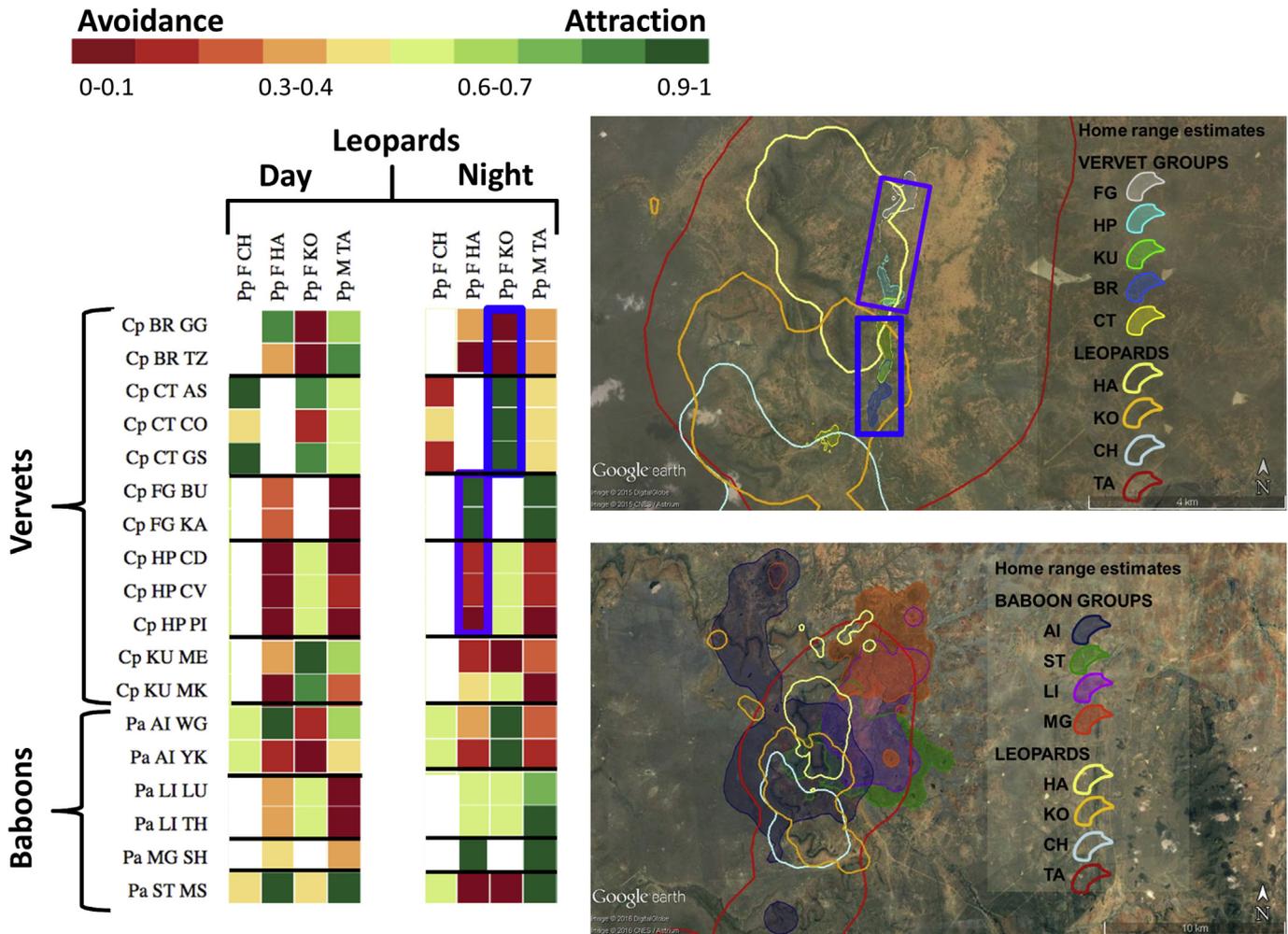
**Figure 3.** Predation on a collared olive baboon by a collared leopard. The baboon's 3D accelerations in the days (left) and minutes (right) before death (21:02–21:04, 8 June, 2014), and GPS data showing the baboon's locations (TH; yellow line) leading up to the attack. Red stars indicate the location of the baboon and the leopard immediately before their encounter. The leopard (TA; aqua line) crossed the Ewaso Nyiro River and moved at least 277 m (138.5 m/min) in the 2 min prior to the kill. He then carried the baboon approximately 90 m before eating her and remaining there for 3.5 h before moving away again.



**Figure 4.** Camera trap photograph of a leopard with an olive baboon killed at its sleeping site.



**Figure 5.** Ratio of vervet approaches to encounters with leopards relative to group size. Approaches indicate lack of predator detection because vervets do not approach leopards they have seen. Despite having fewer individuals to monitor the environment, the failure ratio of smaller vervet groups was not greater than that of larger vervet groups.



**Figure 6.** Home ranges of leopards and primate groups and heat maps of the probability of proximity ranging from attraction (green) to avoidance (red) between individual leopards and primates during the day vs. night. Identity codes indicate species (Cp = *Chlorocebus pygerythrus*, Pa = *Papio anubis*, Pp = *Panthera pardus*), primate group (two letters) or leopard sex (one letter), and individual. Blue and purple rectangles highlight examples of differential attraction/avoidance of certain primate groups within an individual leopard's home range. Home ranges are 99% fixed kernel estimates. Leopard home range sizes = 1753–3492 ha; vervet group home range sizes = 4.5–58 ha; baboon group home range sizes = 2860–7061 ha.

### 3.7. Predation rates and vulnerability

Estimates of the predation rate on vervets by leopards range from 0.02 to 0.05, depending on the measure. For the two vervet groups with known individuals (the smallest and largest groups), the annual predation rate by leopards was collectively 0.05 (2 deaths/42 individuals/12 months). Although theoretical expectations are that larger groups suffer less predation than smaller groups, this was not supported. With one predation event each, the smallest group did not experience more predation than the largest group. For the entire vervet study population, the minimum annual rate of leopard predation was 0.03 (3 deaths/100 individuals/12 months). During all diel periods when collared leopards were near collared vervets at least once and so had a greater opportunity to hunt, the minimum rate of leopard predation was 0.02 (3 deaths over 3 diel periods/118 diel periods). On those particular days when leopards were nearby, i.e., the days when vervets would have been most vulnerable, the minimum rate was 0.05 (3 deaths over 3 12-h days/64 12-h days). Thus, pooling all groups in this study population, when vervets were most vulnerable there was at least a 1-in-20 chance that one would be killed.

Estimates of the leopard predation rate on baboons vary from 0.02 to 0.18. For the baboon group with known individuals, the annual predation rate by leopards was 0.03 (2 deaths/63

individuals/12 months), assuming seven adult males who disappeared were not killed but simply transferred to other groups. That baboon group was nearly twice the size of the largest vervet group, but its annual predation rate was not any lower. For the entire baboon study population, the minimum annual rate of leopard predation was 0.02 (4 deaths/227 individuals/12 months). During all diel periods when collared leopards were near collared baboons at least once and so had a greater opportunity to hunt, the minimum rate was 0.09 (4 deaths over 4 diel periods/45 diel periods). On those particular nights when leopards were nearby, i.e., the nights when baboons would have been most vulnerable, the minimum rate was 0.18 (3 deaths over 3 12-h nights/17 12-h nights). Thus, pooling all study groups in this population, when baboons were most vulnerable there was at least a 1-in-6 chance that one would be killed. Their greater likelihood of being killed compared to vervets, despite fewer encounters, suggests that leopards were more efficient at killing baboons during the particular time period when leopards hunted each species.

## 4. Discussion

Predation on primates is exceedingly challenging to study, partly because it is unpredictable and predators tend to avoid humans, including researchers who typically follow primates on

foot. One consequence has been a heavy reliance on intuitive inferences and assumptions over the years. Our fine-scaled, long-term, remote tracking study with minimized bias from human presence offers the first unadulterated quantitative perspective on spatiotemporal behavioral interactions between large, non-habituated predators and their primate prey, and the first direct quantitative tests of several of these inferences.

Our study shows that even in the absence of human observers, leopards and primates still encountered each other relatively rarely and predation rates were low. With five vervet groups, four baboon groups, and four leopards under surveillance for 688 leopard-primate diel periods, and covering an area of over 130 km<sup>2</sup>, the low encounter and predation rates were less a reflection of sampling intensity than the nature of the topic. We note, however, that our regularly censused study groups, at least, did not experience the episodically intense predation that has been reported elsewhere (Busse, 1980; Isbell, 1990; Isbell et al., 2009). In addition, more leopards occurred in the study area than were collared (e.g., Fig. 4; Wilmers et al., 2017), and so encounter rates and some predation rates (those when individual primates were not known and censused) are presented as minimum estimates. Future studies may require a much larger financial investment to determine encounter rates more accurately, but because human presence is required to census individuals, greater accuracy in predation rates will always be hampered by potential observer effects when the predators are not also habituated (Busse, 1980; Isbell, 1994). We have no reason to believe that our other results were skewed by sampling.

Perceived risk has been popular to study in recent years in recognition that predators can also exert non-lethal effects on prey fitness (Lima, 1998; Creel and Christianson, 2008). There is not yet a consensus on how to measure perceived risk, but it is generally measured using various types of antipredator behavior (Moll et al., 2017). While perceived risk is important for understanding prey behavior, it may not reflect actual risk (Schneier, 2003). Focusing on perceived risk may also be the only option when predator-prey interactions are affected by human presence and cannot be studied directly. Unusually, because we were not limited in that way but were limited in observing prey antipredator behavior (to avoid affecting predator behavior), we focus more on actual risk and vulnerability. Vulnerabilities are weaknesses of prey that can be exploited by predators. For example, sleeping in trees or on cliffs is an antipredator behavior that for vervets and baboons likely reduces both the perceived and actual risk of predation, but baboons were also most vulnerable at their sleeping sites and were more vulnerable than vervets there because leopards hunted them at their sleeping sites.

#### 4.1. What increases vulnerability to predation?

Treves (1999) argued that predation has not been a uniform selection pressure on primate social systems because different predator classes require different responses from the same individual. Our results underscore and extend this argument by also showing that, within the same predator species, individuals often did not behave uniformly over time even toward the same primate group. The temporal variation we found in leopard relationships with primate groups, both during the diel period and over months, is consistent with the reputation of leopards as flexible predators (Hunter et al., 2013). Non-primate-related factors, e.g., other predators, other prey, and life history considerations (e.g., Wilmers et al., 2017), also undoubtedly contribute to variation in leopard-primate relationships by influencing leopard movements, and perhaps this spatial and temporal unpredictability contributes to their reputation as formidable predators of primates (Cowlshaw,

1994; Isbell, 1994; Hart and Sussman, 2005). Nonetheless, nearly ingrained in primatology is that several traits, including large group size and large body size, are evolutionary consequences of directional selection from predation pressure.

Individuals in smaller primate groups are argued to be more vulnerable than those in larger groups, in part because having fewer individuals nearby to monitor the environment is expected to increase the likelihood that predators will be missed or not detected in time for the prey to take evasive action (van Schaik, 1983; van Schaik et al., 1983). Vigilance is generally used as a proxy for the likelihood of predator detection and there is strong support for a positive group-size effect on vigilance in non-primates, suggesting that predation risk can be reduced by living in larger groups (Caro, 2005). However, the evidence is much less supportive in primates (Treves, 2000). Using primate movement toward leopards as a more direct measure of predator (non-) detection than vigilance, we found that larger vervet groups were as likely as smaller groups to fail to detect leopards and that baboon groups, even though they were larger, failed more often than vervet groups to detect leopards, results that further question the 'more eyes' benefit of larger primate groups in reducing predation risk, at least from leopards.

This leads us to ask whether the 'more eyes' benefit found in many species may, in fact, be dependent on predator hunting style. Indeed, every study with a positive group-size effect on predator detection in birds and mammals in Caro's (2005) review involved unconcealed humans as they approached or predators that do not rely on ambush or crypsis to hunt. To examine the 'more eyes' hypothesis thoroughly, more studies involving ambush or cryptic sit-and-wait predators are needed. Consistent with the present study, larger groups of captive rhesus macaques (*Macaca mulatta*) did not detect a stationary snake model, simulating a sit-and-wait predator, more often than did smaller groups (Etting et al., 2014).

Furthermore, smaller groups, smaller body size, and more encounters are predicted to increase the likelihood of predation. However, we found that smaller groups (both within vervets and between primate species), smaller body size (between species), and higher encounter rates with leopards did not actually increase predation rates, the latter because leopards were apparently not always motivated to hunt primates when they were nearby. The lack of a group-size effect on predation rates in this study was also observed in vervets in southern Kenya (Isbell and Young, 1993; Isbell, 1994) and in multiple forest-living cercopithecoid species in Tai Forest, Côte d'Ivoire, although in the latter a trend toward a positive correlation between group size and leopard predation rates was noted (Zuberbühler and Jenny, 2002; but see; Shultz et al., 2004). Hill and Dunbar (1998) argued that no group-size effect should be expected if predation rates reflect residual mortality after prey have implemented their antipredator strategies, a view that is consistent with our distinction between vulnerability and perceived risk.

We found differences in prey species vulnerability only in the diel timing of predation, which was a result of differential influences affecting the motivation of leopards to hunt: leopards are more effectively discouraged from hunting baboons than vervets during the day because baboons have the potential to preemptively attack them. Baboons are more attractive than vervets to leopards at night, however, perhaps because their limited night vision makes a preemptive attack difficult, and, when in sleeping trees, their larger body size reduces their ability to hide within dense vegetation and to escape to terminal branches that may be inaccessible to leopards. Their larger body size also places them well within the range of leopards' preferred prey body sizes. Indeed, during each species' most vulnerable time period, baboons were more likely to be killed than vervets despite their larger body and group sizes. Ultimately,

however, across all time periods, neither species was more vulnerable than the other, thus perhaps exemplifying two equally effective adaptive strategies, with larger body size more protective than smaller body size during the day but more attractive to leopards at night.

It is surprising that leopards were more motivated to hunt vervets during the day, given that leopards are considered nocturnal hunters (Bailey, 1993), they were photographed by camera traps mostly at night at our study site (Isbell and Bidner, 2016; unpub. data), and other field studies reported indirect evidence that leopards killed vervets at night (Cheney et al., 1988; Isbell et al., 2009). The temporal shift in predation from night to day likely occurred in response to the absence of observers near primate groups during the day (Isbell and Young, 1993). If this is so, leopards that become habituated to humans are also expected to hunt diurnally. That the leopard whose home range included the core facilities of the MRC killed a vervet there at midday (Fig. 2), as people were actively walking about, may be a case in point. A study that minimized human presence by tracking two forest-living leopards with radiotelemetry also found they were more active during the day (Zuberbühler and Jenny, 2002).

Our results also do not support the hypothesis that vulnerability to predation increases for primates with greater distance from refuges (Crook and Gartlan, 1966; Dunbar, 1988; Clutton-Brock and Harvey, 1977; Cowlshaw, 1997; Willems and van Schaik, 2017), at least during the day. For vervet groups, actually being in trees likely does help reduce predation as the three vervets who died of confirmed or suspected leopard predation died when they were not in trees. However, once vervets are out of trees, their relative proximity to those refuges likely matters little either for the victim, who will have little opportunity to flee because leopards are ambush hunters, or for its groupmates, who will have sufficient time to run into trees regardless of the distance because the leopard will be focused on carrying off and eating its prey (Figs. 2 and 3). This applies to baboons as well, but importantly, they were not more vulnerable farther away from tall trees or cliffs during the day also likely due to their willingness to launch preemptive and counter-attacks (Cowlshaw, 1994; Cheney et al., 2004; this study). In fact, all predation events on baboons occurred at 'refuges', including the only known daytime predation event.

#### 4.2. Using predator-prey interactions to infer hominin antipredator behavior

In semiarid habitats of Plio-Pleistocene East Africa, hominins, with their larger bodies (as compared to baboons; McHenry, 1994; Palombit, 2013; this study) and stone tool cultures that undoubtedly included the use of stones as weapons, were probably, like modern-day baboons in similar habitats, not constrained to staying near trees or cliffs for protection against predators during the day as assumed by some models (Blumenschine and Peters, 1998; Winder et al., 2013). Like the baboons in this study, these hominins were probably also more vulnerable to leopards at night than during the day due to their large body size and poor ability to see at night to coordinate defensive attacks. Their vulnerability would have only increased as they became more committed to terrestrial bipedalism and less adept in trees.

Our results suggest that dealing with substantial nocturnal threats on the ground would have been a major concern to early hominins, especially by ~1.8 Ma when hominins became committed to bipedalism (Ruff and Walker, 1993; Wood and Collard, 1999; Harcourt-Smith and Aiello, 2004), but this issue has rarely been addressed in comparison to diurnal threats during competition for food (Blumenschine et al., 1994; Blumenschine and Peters, 1998; Egeland, 2014). One model proposes that controlled

use of fire provided essential protection during ground-sleeping and was a prerequisite for committed bipedalism (Wrangham, 2009). For this to be true, controlled use of fire would have to have occurred before ~1.8 Ma when *Homo ergaster-Homo erectus*, the first hominin(s) fully committed to bipedalism, appeared (Ruff and Walker, 1993; Wood and Collard, 1999). However, even contested evidence suggests that control of fire occurred no earlier than ~1.6 Ma (Gowlett et al., 1981; Brain and Sillen, 1988; Bellomo, 1994; Attwell et al., 2005; Berna et al., 2012; Parker et al., 2016). Cave-sleeping, another option for such early hominins, appears not to have been very protective based on the presence of predator-deposited hominins and potential predators of hominins in cave sites such as Swartkrans (Brain, 1981; Lee-Thorp et al., 2000).

Given the leopards' interest in hunting baboons even on difficult-to-access cliffs and in tall trees at night, as our study revealed, we hypothesize that the construction of protective thorny enclosures similar to 'bomas' used today in East Africa to protect livestock and people from predators at night (Ogada et al., 2003; Woodroffe et al., 2007; Fig. 7) was essential for ground-sleeping hominins, especially before controlled use of fire (see also Kortlandt, 1980). The concept of bomas could have developed as an extension and modification of the great ape practice of building night nests generally in trees, which requires manipulation of tree branches (Wrangham, 2009; Koops et al., 2012; Tagg et al., 2013). Thus, *H. ergaster-H. erectus* and their immediate ancestors had a phylogenetic history of creating nighttime refuges out of vegetation. They also had the raw wood materials and the tools for building bomas when they began sleeping on the ground, and they apparently used their tools at times to cut and saw wood. *Acacia* spp., an important raw material for traditional boma construction today, first appeared in Africa 16.6–11.9 Ma as habitats became more open (Ross, 1981; Bouchenak-Khelladi et al., 2010; Odee et al., 2012). Paleocological investigations thus far indicate *Acacia* spp. were present at hominin fossil sites Koobi Fora, Olduvai, Laetoli, Sterkfontein, and Swartkrans (Avery, 2001; Andrews and Bamford, 2008; Bamford, 2011; Reed and Denys, 2011; Barboni, 2014). Flake tools sharp enough to cut *Acacia* branches appeared by about 3.3–2.6 Ma in eastern Africa (Plummer, 2004; Harmand et al., 2015). Most importantly, and consistent with our suggested correlated timeline for committed bipedalism and boma building, microwear and use-wear analyses at Kenyan sites have identified Oldowan tools that were used to cut wood by 2.0 Ma and saw wood



**Figure 7.** Example of a modern-day boma in eastern Africa, constructed with *Acacia drepanolobium* branches.

by 1.5 Ma (Keeley and Toth, 1981; Lemorini et al., 2014), and phytoliths attributed to *Acacia* spp. have been found on Acheulean handaxes dated to ~1.5 Ma at Peninj in Tanzania (Domínguez-Rodrigo et al., 2001). These handaxes were carried several kilometers, a behavior that, according to Domínguez-Rodrigo et al. (2001), must have been necessary because of the high energy investment in it. The effectiveness of bomas in protecting against nocturnal predators, particularly before controlled use of fire, would appear to justify the high energy investment in tool transport.

Although temporarily occupied bomas constructed of *Acacia* spp. and used mainly as protective sleeping sites (as opposed to more permanent home bases: Isaac, 1978; Rose and Marshall, 1996) may not leave obvious fossil evidence, we suggest that our boma hypothesis could be tested through an examination of tool wear and phytolith presence in conjunction with changes at sites in predator-accumulated fossil assemblages of hominin and non-hominin primates. We predict that both hominin and non-hominin primates will be represented in predator-accumulated assemblages at levels in which stone tools lack microwear consistent with wood cutting or the presence of *Acacia* phytoliths, whereas hominins will be underrepresented at levels in which tools associated with them show evidence of *Acacia* cutting. Swartkrans may provide a good site at which to test the boma hypothesis because variation in the presence of hominins exists in the strata, with predator-deposited baboons, *P. robustus*, and *Homo* appearing in Members 1–3 but with *Homo* underrepresented in Member 3, along with tools in all the strata (Brain, 1981; Watson, 1993; Susman et al., 2005; Pickering et al., 2008).

Our study emphasizes the dynamic relationships between leopards and two very different non-human primate species. The relationships between leopards and many early hominin species were likely equally dynamic, if not more so due to competition for prey resources (e.g., Brain, 1970, 1981; Blumenschine et al., 1994; Werdelin and Lewis, 2013). The effects of such dynamic relationships on human and non-human primate evolution warrant further study. Indeed, pursuing further evidence of nocturnal antipredator strategies, when hominins would have been most vulnerable, may be as important as the pursuit of evidence of food acquisition in understanding the origins and expansion of genus *Homo*. For example, it is not difficult to see how bomas would have both reduced predation from nocturnal predators and increased hominin mobility by reducing their dependency on natural refuges. The ability to erect nighttime refuges wherever *Acacia* spp. occurred, thus obviating the need to return repeatedly to more spatially limited natural sleeping sites, would have allowed hominins to travel more widely across the landscape, a crucial step in furthering the spread of hominins across Africa and beyond. As our study challenges long-standing views on primate antipredator adaptations by examining leopard interactions with two well-studied non-human primates that thrive in relatively arid, predator-rich African environments today, so might future studies expose unexpected ways in which interactions with predators affected the course of human evolution.

## Acknowledgments

The research was conducted under University of California, Davis IACUC protocol #17477 and Kenya Government NACOSTI permit No. P/15/5820/4650. We thank the Kenya Wildlife Service for local affiliation. We also thank D. Simpson, S. Ekwanga, M. Mutinda, G. Omondi, W. Longor, M. Iwata, A. Surmat, M. Snider, W. Fox, and K. VanderWaal for field assistance, D. Rubenstein and L. Frank for the use of their field equipment, M. Kinnaird and T. Young for logistical support in the field, R. Coss, H.W. Greene, M. Grote, D.

Simpson, T. Young, and N. Zwyns for helpful discussions, and K. Veblen for the photograph of a boma. We also appreciate the constructive comments and suggestions offered by the editor, associate editor, two anonymous reviewers, and R. Hill. Funding was provided by the National Science Foundation (grant nos. BCS 99-03949, BCS 1266389), the L.S.B. Leakey Foundation, and the Committee on Research, University of California, Davis, to L.A.I.; JSPS KEKENHI (grant no. 23405016) to A.M.O.; the Wenner-Gren Foundation (grant no. 8386) to L.R.B., and the National Science Foundation (grant nos. IOS-1250895, BCS 1440755, III 1514174) to M.C.C.

## References

- Andrews, P., Bamford, M., 2008. Past and present vegetation ecology of Laetoli, Tanzania. *Journal of Human Evolution* 54, 78–98.
- Attwell, L., Kovarovic, K., Kendal, J.R., 2005. Fire in the Plio-Pleistocene: the functions of hominin fire use, and the mechanistic, developmental and evolutionary consequences. *Journal of Anthropological Sciences* 93, 1–20.
- Avery, D.M., 2001. The Plio-Pleistocene vegetation and climate of Sterkfontein and Swartkrans, South Africa, based on micromammals. *Journal of Human Evolution* 41, 113–132.
- Bailey, T.N., 1993. *The African Leopard: Ecology and Behavior of a Solitary Felid*. Columbia University Press, New York.
- Bamford, M.K., 2011. Late Pliocene woody vegetation of Area 41, Koobi Fora, East Turkana Basin, Kenya. *Review of Palaeobotany and Palynology* 164, 191–210.
- Barboni, D., 2014. Vegetation of northern Tanzania during the Plio-Pleistocene: a synthesis of the paleobotanical evidences from Laetoli, Olduvai, and Peninj hominin sites. *Quaternary International* 322, 264–276.
- Bellomo, R.V., 1994. Methods of determining early hominid behavioral activities associated with the controlled use of fire at Fxj 20 Main, Koobi Fora, Kenya. *Journal of Human Evolution* 27, 173–195.
- Berna, F., Goldberg, P., Horwitz, L.K., Brink, J., Holt, S., Bamford, M., Chazang, M., 2012. Microstratigraphic evidence of in situ fire in the Acheulean strata of Wonderwerk Cave, Northern Cape province, South Africa. *Proceedings of the National Academy of Sciences USA* 109, 1215–1220.
- Bettridge, C.M., Dunbar, R.I.M., 2012. Predation as a determinant of minimum group size in baboons. *Folia Primatologica* 83, 332–352.
- Blumenschine, R.J., Cavallo, J.A., Capaldo, S.D., 1994. Competition for carcasses and early hominid behavioral ecology: a case study and conceptual framework. *Journal of Human Evolution* 27, 197–213.
- Blumenschine, R.J., Peters, C.R., 1998. Archaeological predictions for hominid land use in the paleo-Olduvai Basin, Tanzania, during lowermost Bed II times. *Journal of Human Evolution* 34, 565–607.
- Bouchenak-Khelladi, Y., Maurin, O., Hurter, J., van der Bank, M., 2010. The evolutionary history and biogeography of Mimosoideae (Leguminosae): an emphasis on African acacias. *Molecular Phylogenetics and Evolution* 57, 495–508.
- Brain, C.K., 1970. New finds at the Swartkrans australopithecine site. *Nature* 225, 1112–1119.
- Brain, C.K., 1981. *The Hunters or the Hunted? An Introduction to African Cave Taphonomy*. University of Chicago Press, Chicago.
- Brain, C.K., 1993. A taphonomic overview of the Swartkrans fossil assemblages. In: Brain, C.K. (Ed.), *Transvaal Museum Monograph 8: Swartkrans: a Cave's Chronicle of Early Man*. Transvaal Museum, Pretoria, pp. 257–264.
- Brain, C.K., Sillen, A., 1988. Evidence from the Swartkrans cave for the earliest use of fire. *Nature* 336, 464–466.
- Brown, G.R., 2001. Using proximity measures to describe mother-infant relationships. *Folia Primatologica* 72, 80–84.
- Busse, C., 1980. Leopard and lion predation upon chacma baboons living in the Moremi Wildlife Reserve. *Botswana Notes and Records* 12, 15–21.
- Calenge, C., 2006. The package adehabitat for the R software: a tool for the analysis of space and habitat use by animals. *Ecological Modelling* 197, 516–519.
- Caro, T., 2005. *Antipredator Defenses in Birds and Mammals*. University of Chicago Press, Chicago.
- Cheney, D.L., Seyfarth, R.M., 1981. Selective forces affecting the predator alarm calls of vervet monkeys. *Behaviour* 76, 25–61.
- Cheney, D.L., Seyfarth, R.M., Andelman, S.J., Lee, P.C., 1988. Reproductive success in vervet monkeys. In: Clutton-Brock, T.H. (Ed.), *Reproductive Success*. University of Chicago Press, Chicago, pp. 384–402.
- Cheney, D.L., Seyfarth, R.M., Fischer, J., Beehner, J., Bergman, T., Johnson, S.E., Kitchen, D.M., Palombit, R.A., Rendall, D., Silk, J.B., 2004. Factors affecting reproduction and mortality among baboons in the Okavango Delta, Botswana. *International Journal of Primatology* 25, 401–428.
- Cheney, D.L., Wrangham, R.W., 1987. Predation. In: Smuts, B.B., Cheney, D.L., Seyfarth, R.M., Wrangham, R.W., Struhsaker, T.T. (Eds.), *Primate Societies*. University of Chicago Press, Chicago, pp. 227–239.
- Clutton-Brock, T.H., Harvey, P.H., 1977. *Primate ecology and social organization*. *Journal of Zoology*, London 183, 1–39. London.
- Cowlshaw, G., 1994. Vulnerability to predation in baboon populations. *Behaviour* 131, 293–304.

- Cowlishaw, G., 1997. Refuge use and predation risk in a desert baboon population. *Animal Behaviour* 54, 241–253.
- Creel, S., Christianson, D., 2008. Relationships between direct predation and risk effects. *Trends in Ecology and Evolution* 23, 194–201.
- Crofoot, M.C., Kays, R.W., Wikelski, M., 2015. Data from “Shared decision-making drives collective movement in wild baboons. Movebank Data Repository. <https://doi.org/10.5441/001/1.kn0816jn>.
- Crook, J.H., Gartlan, J.S., 1966. Evolution of primate societies. *Nature* 210, 1200–1203.
- DeVore, I., Washburn, S.L., 1963. Baboon ecology and human evolution. In: Howell, F.C., Bourlière, F. (Eds.), *African Ecology and Human Evolution*. Aldine, Chicago, pp. 335–367.
- Dominguez-Rodrigo, M., Serrallonga, J., Juan-Tresserras, J., Alcalá, L., Luque, L., 2001. Woodworking activities by early humans: a plant residue analysis on Acheulian stone tools from Peninj (Tanzania). *Journal of Human Evolution* 40, 289–299.
- Dunbar, R.I.M., 1988. *Primate Social Systems*. Cornell University Press, Ithaca.
- Egeland, C.P., 2014. Taphonomic estimates of competition and the role of carnivore avoidance in hominin site use within the Early Pleistocene Olduvai Basin. *Quaternary International* 322–323, 95–106.
- Elton, S., 2007. Forty years and still going strong: the use of hominin-cercopithecoid comparisons in palaeoanthropology. *Journal of the Royal Anthropological Institute* 12, 19–38.
- Etting, S.F., Isbell, L.A., Grote, M.N., 2014. Factors increasing snake detection and perceived threat in captive rhesus macaques (*Macaca mulatta*). *American Journal of Primatology* 76, 135–145.
- Fay, J.M., Carroll, R., Peterhans, J.C.K., Harris, D., 1995. Leopard attack on and consumption of gorillas in the Central African Republic. *Journal of Human Evolution* 29, 93–99.
- Frank, L., Simpson, D., Woodroffe, R., 2003. Foot snares: An effective method for capturing African lions. *Wildlife Society Bulletin* 31, 309–314.
- Grobler, J.P., Turner, T.R., 2010. A novel trap design for the capture and sedation of vervet monkeys (*Chlorocebus aethiops*). *South African Journal of Wildlife Research* 40, 163–168.
- Gowlett, J.A.J., Harris, J.W.K., Walton, D., Wood, B.A., 1981. Early archaeological sites, hominin remains and traces of fire from Chesowanja, Kenya. *Nature* 294, 125–129.
- Harcourt-Smith, W.E.H., Aiello, L.C., 2004. Fossils, feet and the evolution of human bipedal locomotion. *Journal of Anatomy* 204, 403–416.
- Harmand, S., Lewis, J.E., Feibel, C.S., Lepre, C.J., Prat, S., Lenoble, A., Boës, Z., Quinn, R.L., Brenet, B., Arroyo, A., Taylor, N., Clément, S., Daver, G., Brugal, J.-P., Leakey, L., Mortlock, R.A., Wright, J.D., Lokorodi, S., Kirwa, C., Kent, D.V., Roche, H., 2015. 3.3-million-year-old stone tools from Lomekwi 3, West Turkana, Kenya. *Nature* 521, 310–315.
- Hart, D.L., Sussman, R.W., 2005. *Man the Hunted: Primates, Predators, and Human Evolution*. Westview Press, Boulder.
- Hart, J.A., Katembo, M., Punga, K., 1996. Diet, prey selection and ecological relations of leopard and golden cat in the Ituri Forest, Zaire. *African Journal of Ecology* 34, 364–379.
- Hayward, M.W., Henschel, P., O'Brien, J.O., Hofmeyr, M., Balme, G., Kerley, G.I.H., 2006. Prey preferences of the leopard (*Panthera pardus*). *Journal of Zoology* 270, 298–313.
- Hill, R.A., Dunbar, R.I.M., 1998. An evaluation of the roles of predation rate and predation risk as selective pressures on primate grouping behaviour. *Behaviour* 135, 411–430.
- Hunter, L., Henschel, P., Ray, J.C., 2013. *Panthera pardus* - leopard. In: Kingdon, J., Hoffman, M. (Eds.), *The Mammals of Africa*, Vol. 5. Carnivores, Pangolins, Equids and Rhinoceroses. Bloomsbury Publishing, London, pp. 159–168.
- Isaac, G., 1978. The food-sharing behavior of protohuman hominids. *Scientific American* 238, 90–108.
- Isbell, L.A., 1990. Sudden short-term increase in mortality of vervet monkeys (*Cercopithecus aethiops*) due to leopard predation in Amboseli National Park, Kenya. *American Journal of Primatology* 21, 41–52.
- Isbell, L.A., 1994. Predation on primates: ecological causes and evolutionary consequences. *Evolutionary Anthropology* 3, 61–71.
- Isbell, L.A., Bidner, L.R., 2016. Vervet monkey (*Chlorocebus pygerythrus*) alarm calls to leopards (*Panthera pardus*) function as a predator deterrent. *Behaviour* 153, 591–606.
- Isbell, L.A., Pruett, J.D., Lewis, M., Young, T.P., 1998. Locomotor activity differences between sympatric patas monkeys (*Erythrocebus patas*) and vervet monkeys (*Cercopithecus aethiops*): implications for the evolution of long hindlimb length in *Homo*. *American Journal of Physical Anthropology* 105, 199–207.
- Isbell, L.A., Young, T.P., 1993. Human presence reduces predation in a free-ranging vervet monkey population in Kenya. *Animal Behaviour* 45, 1233–1235.
- Isbell, L.A., Young, T.P., Jaffe, K.E., Carlson, A.A., Chancellor, R.L., 2009. Demography and life histories of sympatric patas monkeys (*Erythrocebus patas*) and vervets (*Cercopithecus aethiops*) in Laikipia, Kenya. *International Journal of Primatology* 30, 103–124.
- Jolly, C.J., Phillips-Conroy, J.E., Mueller, A.E., 2003. Trapping primates. In: Setchell, J.M., Curtis, D.J. (Eds.), *Field and Laboratory Methods in Primatology: a Practical Guide*. Cambridge University Press, Cambridge, pp. 110–121.
- Keeley, L.H., Toth, N., 1981. Microwear polishes on early stone tools from Koobi Fora, Kenya. *Nature* 293, 464–465.
- Kernohan, B.J., Gitzen, R.A., Millsapugh, J.J., 2001. Analysis of animal space use and movements. In: Millsapugh, J.J., Marzluff, J.M. (Eds.), *Radio-Tracking Animal Populations*. Academic Press, San Diego, pp. 125–166.
- Koops, K., McGrew, W.C., de Vries, H., Matsuzawa, T., 2012. Nest-building by chimpanzees (*Pan troglodytes verus*) at Seringbara, Nimba Mountains: anti-predation, thermoregulation, and antivector hypotheses. *International Journal of Primatology* 33, 356–380.
- Kortlandt, A., 1980. How might early hominids have defended themselves against large predators and food competitors? *Journal of Human Evolution* 9, 79–112.
- Lee-Thorp, J., Thackeray, J.F., van der Merwe, N., 2000. The hunters and the hunted revisited. *Journal of Human Evolution* 39, 565–576.
- Lemorini, C., Plummer, T.W., Braun, D.R., Crittenden, A.N., Ditchfield, P.W., Bishop, L.C., Hertel, R., Oliver, J.S., Marlowe, F.W., Schoeninger, M.J., Potts, R., 2014. Old stones' song: use-wear experiments and analysis of the Oldowan quartz and quartzite assemblage from Kanjera South (Kenya). *Journal of Human Evolution* 72, 10–25.
- Li, Z., Ding, B., Wu, F., Kin Hou Lei, T., Kays, R.W., Crofoot, M.C., 2013. Attraction and avoidance detection from movements. *Proceedings of the Vldb Endowment* 5, 157–168.
- Lima, S.L., 1998. Nonlethal effects in the ecology of predator-prey interactions. *Bioscience* 48, 25–34.
- Lowry, R., 1998. *VassarStats: Website for Statistical Computation*. <http://vassarstats.net>.
- McHenry, H.M., 1991. Petite bodies of the “robust” australopithecines. *American Journal of Physical Anthropology* 86, 445–454.
- McHenry, H.M., 1992. Body size and proportions in early hominids. *American Journal of Physical Anthropology* 87, 407–431.
- McHenry, H.M., 1994. Behavioral ecological implications of early hominid body size. *Journal of Human Evolution* 27, 77–87.
- Melnick, D.J., Pearl, M.C., 1987. Cercopithecines in multimale groups: genetic diversity and population structure. In: Smuts, B.B., Cheney, D.L., Seyfarth, R.M., Wrangham, R.W., Struhsaker, T.T. (Eds.), *Primate Societies*. University of Chicago Press, Chicago, pp. 121–134.
- Miller, L.E., Treves, A., 2007. Predation on primates: past studies, current challenges, and directions for the future. In: Campbell, C.J., Fuentes, A., MacKinnon, L.C., Panger, M., Bearder, S.K. (Eds.), *Primates in Perspective*. Oxford University Press, New York, pp. 525–543.
- Moll, R.J., Redilla, K.M., Mudumba, T., Muneza, A.B., Gray, S.M., Abade, L., Hayward, M.W., Millsapugh, J.J., Montgomery, R.A., 2017. The many faces of fear: a synthesis of the methodological variation in characterizing predation risk. *Journal of Animal Ecology* 86, 749–765.
- Ngoprasert, D., Lynam, A.J., Gale, G.A., 2007. Human disturbance affects habitat use and behavior of Asiatic leopard *Panthera pardus* in Kaeng Krachan National Park, Thailand. *Oryx* 41, 343–351.
- Odee, D.W., Telford, A., Wilson, J., Gaye, A., Cavers, S., 2012. Plio-Pleistocene history and phylogeography of *Acacia senegal* in dry woodlands and savannahs of sub-Saharan tropical Africa: evidence of early colonization and recent range expansion. *Heredity* 109, 372–382.
- Ogada, M.O., Woodroffe, R., Oguge, N.O., Frank, L.G., 2003. Limiting depredation by African carnivores: the role of livestock husbandry. *Conservation Biology* 17, 1521–1530.
- Palombit, R.A., 2013. *Papio anubis* – olive baboon. In: Butynski, T.M., Kingdon, J., Kalina, J. (Eds.), *Mammals of Africa*, Vol. 2. Primates. Bloomsbury Publishing, London, pp. 233–239.
- Parker, C.H., Keefe, E.R., Herzog, N.M., O'Connell, J.F., Hawkes, K., 2016. The pyrophilic primate hypothesis. *Evolutionary Anthropology* 25, 54–63.
- Pickering, T.R., Egeland, C.P., Dominguez-Rodrigo, M., Brain, C.K., Schnell, A., 2008. Testing the “shift in the balance of power” hypothesis at Swartkrans, South Africa: hominid cave use and subsistence behavior in the Early Pleistocene. *Journal of Anthropological Archaeology* 27, 30–45.
- Plummer, T., 2004. Flaked stones and old bones: biological and cultural evolution at the dawn of technology. *Yearbook of Physical Anthropology* 47, 118–164.
- Reed, D.N., Denys, C., 2011. The taphonomy and paleoenvironmental implications of the Laetoli micromammals. In: Harrison, T. (Ed.), *Paleontology and Geology of Laetoli: Human Evolution in Context, Geology, Geochronology, Paleocology and Paleoenvironment*, vol. 1. Springer, New York, pp. 265–278.
- Reed, K.E., 1997. Early hominid evolution and ecological change through the African Plio-Pleistocene. *Journal of Human Evolution* 32, 289–322.
- Rose, L., Marshall, F., 1996. Meat eating, hominid sociality, and home bases revisited. *Current Anthropology* 37, 307–338.
- Ross, J.H., 1981. An analysis of the African *Acacia* species: their distribution, possible origins and relationships. *Biotalia* 13, 398–413.
- Ruff, C.B., Walker, A.C., 1993. Body size and body shape. In: Walker, A.C., Leakey, R.E. (Eds.), *The Nariokotome Homo erectus Skeleton*. Harvard University Press, Cambridge, pp. 234–265.
- Schaller, G.B., 1963. *The Mountain Gorilla*. University of Chicago Press, Chicago.
- Schneier, B., 2003. *Beyond Fear: Thinking Sensibly About Security in an Uncertain World*. Copernicus Books, New York.
- Shultz, S., Noë, R., McGraw, W.S., Dunbar, R.I.M., 2004. A community-level evaluation of the impact of prey behavioural and ecological characteristics on predator diet composition. *Proceedings of the Royal Society London B* 271, 725–732.
- Sillen, A., Lee-Thorp, J.A., 1994. Trace element and isotopic aspects of predator-prey relationships in terrestrial foodwebs. *Palaeogeography, Palaeoclimatology, Palaeoecology* 107, 243–255.
- Stankovich, T., Coss, R.G., 2007. The re-emergence of felid camouflage with the decay of predator recognition in deer under relaxed selection. *Proceedings of the Royal Society London B* 247, 175–182.
- Strum, S.C., 2012. Darwin's monkey: why baboons can't become human. *Yearbook of Physical Anthropology* 55, 3–23.

- Susman, R.L., de Ruiter, D., Brain, C.K., 2005. Recently identified postcranial remains of *Paranthropus* and early *Homo* from Swartkrans Cave, South Africa. *Journal of Human Evolution* 41, 607–629.
- Tagg, N., Willie, J., Petre, C.-A., Haggis, O., 2013. Ground night nesting in chimpanzees: new insights from central chimpanzees (*Pan troglodytes troglodytes*) in south-east Cameroon. *Folia Primatologica* 85, 362–383.
- Treves, A., 1999. Has predation shaped the social systems of arboreal primates? *International Journal of Primatology* 20, 35–67.
- Treves, A., 2000. Theory and method in studies of vigilance and aggregation. *Animal Behaviour* 60, 711–722.
- Treves, A., Naughton-Treves, L., 1999. Risk and opportunity for humans coexisting with large carnivores. *Journal of Human Evolution* 36, 275–282.
- Turner, A., 1990. The evolution of the guild of larger terrestrial carnivores during the Plio-Pleistocene in Africa. *Geobios* 23, 349–368.
- Turner, A., Anton, M., 1997. *The Big Cats and their Fossil Relatives*. Columbia University Press, New York.
- Uphyrkina, O., Johnson, W.E., Quigley, H., Miquelle, D., Marker, L., Bush, M., O'Brien, S.J., 2001. Phylogenetics, genome diversity and origin of modern leopard, *Panthera pardus*. *Molecular Ecology* 10, 2617–2633.
- van Schaik, C.P., 1983. Why are diurnal primates living in groups? *Behaviour* 87, 120–144.
- van Schaik, C.P., van Noordwijk, M.A., Warsono, B., Sutriyono, E., 1983. Party size and early detection of predators in Sumatran forest primates. *Primates* 24, 211–221.
- Watson, V., 1993. Composition of the Swartkrans bone accumulations, in terms of skeletal parts and animals represented. In: Brain, C.K. (Ed.), *Transvaal Museum Monograph 8: Swartkrans: a Cave's Chronicle of Early Man*. Transvaal Museum, Pretoria, pp. 35–73.
- Werdelin, L., Lewis, M.E., 2005. Plio-Pleistocene Carnivora of eastern Africa: species richness and turnover patterns. *Zoological Journal of the Linnean Society* 144, 121–144.
- Werdelin, L., Lewis, M.E., 2013. Temporal change in functional richness and evenness in the eastern African Plio-Pleistocene carnivoran guild. *PLoS One* 8, e57944.
- Wikelski, M., Kays, R., 2017. Movebank: archive, analysis and sharing of animal movement data. <https://www.movebank.org> (accessed 2.02.2018).
- Willems, E.P., van Schaik, C.P., 2017. The social organization of *Homo ergaster*: inferences from anti-predator responses in extant primates. *Journal of Human Evolution* 109, 11–21.
- Wilmers, C.C., Isbell, L.A., Suraci, J., Williams, T.M., 2017. Energetics-informed behavioral states reveal the drive to kill in African leopards. *Ecosphere* 8, e01850.
- Winder, I.C., King, G.C.P., Deves, M., Bailey, G.N., 2013. Complex topography and human evolution: the missing link. *Antiquity* 87, 333–349.
- Wood, B., Collard, M., 1999. The changing face of Genus *Homo*. *Evolutionary Anthropology* 8, 195–207.
- Woodroffe, R., Frank, L.G., Lindsey, P.A., ole Ranah, S.M.K., Romanach, S., 2007. Livestock husbandry as a tool for carnivore conservation in Africa's community rangelands: a case-control study. *Biodiversity and Conservation* 16, 1245–1260.
- Wrangham, R.W., 2009. *Catching Fire: How Cooking Made Us Human*. Basic Books, New York.
- Young, T.P., Okello, B., Kinyua, D., Palmer, T.M., 1998. KLEE: a long-term multi-species herbivore exclusion experiment in Laikipia, Kenya. *African Journal of Range and Forage Science* 14, 92–104.
- Zuberbühler, K., Jenny, D., 2002. Leopard predation and primate evolution. *Journal of Human Evolution* 43, 873–886.