



# Vervet monkey (*Chlorocebus pygerythrus*) alarm calls to leopards (*Panthera pardus*) function as a predator deterrent

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## Abstract

Behavioural predator–prey interactions are difficult to study, especially when predators avoid humans. To gain greater understanding of their dynamism, we conducted a 14-month field study in which we minimized human presence by employing acoustic recorders and camera traps, along with GPS collars deployed on vervet monkeys (*Chlorocebus pygerythrus*) and leopards (*Panthera pardus*) in Laikipia, Kenya. Recordings at the vervets' sleeping site revealed that they gave 'leopard' alarm calls most frequently near dusk and dawn, whereas photographs showed that leopards approached vervets more closely at night, when the monkeys alarm-called less often. GPS data showed that after vervets alarm-called, leopards within 200 m quickly moved away, changing direction, but when vervets did not alarm-call, leopards continued moving forward. These results reveal that vervets' leopard alarm calls function as a predator deterrent in addition to a conspecific warning call.

## Keywords

anti-predator behaviour, predator deterrence, pursuit deterrence, human presence, primates, carnivorans, remote observations, predation risk.

## 1. Introduction

The study of predator–prey interactions has a long history (Berryman, 1992), but the study of behavioural predator–prey interactions has tended toward smaller organisms, partly because of their greater tractability under laboratory conditions (e.g., Savino & Stein, 1982; Hammond et al., 2012). The

challenges of directly observing predation in the wild have led to creative approaches to studying behavioural predator–prey interactions. A common approach has been the simulation experiment in which prey animals are exposed to visual or acoustic models of their predators, human surrogates for predators, or alarm calls from conspecifics.

One highly influential and now classic simulation experiment involved playing back to vervet monkeys (*Chlorocebus pygerythrus*) recordings of their own alarm calls and observing their responses (Seyfarth et al., 1980a, b). Vervets were found to have alarm calls that are functionally referential, i.e., the alarm calls are acoustically unambiguous, they are given in the context of particular predators with different hunting styles, and conspecifics respond in an appropriately evasive manner to each type of alarm call (Seyfarth et al., 1980a, b). When a recording of a ‘leopard’ alarm call was played, vervets on the ground often ran for the safety of trees. When an ‘eagle’ alarm call was played, vervets in trees often moved quickly down from the canopy. Finally, when a ‘snake’ alarm call was played, vervets on the ground often stood bipedally and looked on the ground around themselves (Seyfarth et al., 1980a, b). Thus, their alarm calls clearly function as warning calls to conspecifics about specific predator types. Since vervet groups are composed of related adult females, their offspring, and multiple adult males, some of whom could be sires, many conspecifics receiving the warnings are also close relatives (Cheney & Seyfarth, 1981).

It has been argued for rodents that alarm calls evolved into a warning signal to benefit kin after initially evolving to communicate with predators as a means to deter them (Shelley & Blumstein, 2005). Many other prey taxa also signal detection visually or acoustically to predators, which then give up hunting (the ‘pursuit deterrence’ or ‘predator deterrent’ function of alarm calls: Woodland et al., 1980; Caro, 1989, 1995, 2005; Hasson, 1991; Zuberbühler et al., 1999; Clark, 2005; Stankowich & Coss, 2008).

Limited evidence suggests that vervets’ leopard alarm calls also serve a function beyond alerting conspecifics. Individual vervets give alarm calls most often to the predators to which they themselves are most vulnerable, not to those to which others of different age classes are most vulnerable (Cheney & Seyfarth, 1981), and they continue to give alarm calls to leopards well after everyone has spotted the predator (Cheney & Seyfarth, 1990). These responses would not be expected if the alarm calls function only to warn relatives and other group members. Male vervets sometimes give leopard

alarm calls to other vervet groups, strange males, and other predators but only rarely (Seyfarth et al., 1980b; Cheney & Seyfarth, 1990; Enstam & Isbell, 2002). Thus, the calls are reliable indicators that a leopard (*Panthera pardus*) has been detected (Cheney & Seyfarth, 1990; Price et al., 2014), and it is possible that the calls function in another way that is directly associated with leopards, one of which could be predator deterrence.

Several other species of Old World monkeys (e.g., *Procolobus*, *Colobus*, *Cercopithecus* and *Cercocebus*) also give loud alarm calls when they detect leopards (Zuberbühler et al., 1997, 1999). In Tai Forest, Ivory Coast, a radio-collared leopard moved away from groups of monkeys sooner than expected when the monkeys gave alarm calls (Zuberbühler et al., 1999). Since leopards are mainly ambush hunters, relying heavily on secrecy and stealth to kill their prey, it was suggested that the alarm calls function as a predator deterrent, causing the leopards for the time being to give up hunting (Zuberbühler et al., 1999). Moreover, since alarm calls can also be used by heterospecifics as a warning signal that a predator is nearby ('eavesdropping': Lea et al., 2008; Müller & Manser, 2008; Kitchen et al., 2010), leopards might find it more profitable to leave rather than remain in the area.

If vervet alarm calls that are given upon detecting leopards function as a predator deterrent, leopards should respond to the alarm calls in such a way that it reduces the vervets' risk of predation while also reducing the cost to the leopards. Leopards are thus predicted to avoid approaching or to move away when vervets give leopard alarm calls. We tested this prediction in the present study with a multi-modal remote approach using camera traps, acoustic recorders, and GPS radio-collars in place of direct observation to minimize the potential for human interference in the movements of leopards.

## 2. Methods

### 2.1. Study site

We collected the data presented here from December 2013–January 2015 in the semi-arid savannah-bushlands and -woodlands around Mpala Research Centre on the Laikipia Plateau of central Kenya (0.29°N, 33.90°E). The mammalian community in the area is nearly intact; at least 14 species of ungulates and six species of large carnivores inhabit the area. We concentrated on a grove of *Acacia xanthophloea* on the edge of a bow in the Ewaso Nyiro River (0.32°N, 36.91°E) that was the main sleeping site for one group of vervets.

## 2.2. *Study subjects*

Vervets and leopards moving in and around the sleeping site were studied via time-stamped photographs from camera traps, time-stamped acoustic recordings, time-stamped GPS data, and direct observation. One group of 30–35 habituated and individually identified vervets (8–9 adult males, 10–12 adult females, 1–3 subadult males, 11 juveniles and 0–8 infants) slept there on 349 of 358 (97%) nights. Examination of spot patterns from 59 distinct photographic events of leopards indicated that at least eight leopards included the vervets' sleeping site in their home ranges. Seven were identified as individuals: one large adult male, two young adult males approximately two years old, and three adult females, one of whom was observed with a large cub.

## 2.3. *Remote monitoring equipment*

Following Grobler & Turner (2010), we trapped and placed GPS collars (Savannah Tracking, Inc., Nairobi, Kenya) on three adult females from the vervet group. Because vervets live in cohesive groups, the locations of these collared individuals were representative of the general location of the entire group. Following Frank et al. (2003), we also trapped and placed GPS collars on four leopards, two of whom included the sleeping site within their home ranges. All collars were programmed to take GPS fixes synchronously every 15 min continuously throughout the life of the collars. We carried a GPS device (Garmin GPSMAP 62 Handheld Navigator, Olathe, KS, USA) to record our own locations at 15-min intervals while we censused the vervet group at the sleeping site and when we searched for collared animals.

We positioned the acoustic recorder (Songmeter SM2; Wildlife Acoustics, Maynard, MA, USA) in the centre of the grove of sleeping trees. We configured it to record at 48 000 MHz sampling frequency from 17:00–08:00 every night. It recorded in separate 1-h digital audio files all vocalizations at the sleeping site, including vervets' leopard alarm calls.

We programmed three cameras (Reconyx Hyperfire PC900 and Rapidfire RM45; Reconyx, Holmen, WI, USA), to run continuously day and night, taking photographs in bouts of three/s when triggered by movement and heat. One camera was placed at the vehicle entrance to the sleeping site specifically to record arrivals and departures of human visitors. This was located on the edge of the grove of trees slept in by the vervets. Another camera was attached to a sleeping tree across the glade from the first camera,

and a third camera was placed on a dead tree stump near a weir used by animals to cross the river. Both were well within the grove of trees in which the vervets regularly slept.

#### 2.4. *Ethical note*

This research was approved under IACUC protocol No. 17477 at the University of California, Davis, CA, USA, conformed to the guidelines of the American Society of Mammalogists (Sikes et al., 2011), and was approved in Kenya by the Kenya Wildlife Service, National Council for Science and Technology, and National Commission for Science, Technology, and Innovation (NACOSTI/P/15/5820/4650).

#### 2.5. *Data collection and analyses*

We used a base station (e-obs, Grünwald, Germany) with an omnidirectional marine antenna (cx1 900-3LW: Procom, Frederikssund, Denmark) or nine-element yagi antenna (YAGI-869A: Low Power Radio Solutions, Witney, UK) to download GPS data remotely. We tested the accuracy of the collars by examining 1122 readings from two stationary collars. The mean difference  $\pm$  SD in distance between readings was  $11 \pm 20$  m;  $N = 275$  and  $12 \pm 10$  m;  $N = 847$ . The GPS units successfully acquired 36 115 location fixes for the two leopards that visited the sleeping site and 44 839 for the three vervets.

We obtained 4538 functional 1-h audio files spanning 305 nights, and trained 102 assistants to listen to and screen the files for leopard alarm calls. To avoid false positives, LAI double-checked all files reported to have leopard alarm calls. To minimize false negatives, LAI and at least one other assistant spot-checked 851 files (19% of the total). Spot-checking was random except that all files of assistants found to have missed leopard alarm calls were screened again by LAI or other assistants. False negatives were found on four files (0.47%) that were spot-checked. All were recordings from just before sunset or after sunrise when birds' vocalizations were at their peak, making it more difficult to hear vervets' alarm calls. Thus, if any alarm calls were missed on files that were not double-checked, they were likely to have been during the hours when most alarm calls were already noted (see Results), making our results more conservative. Alarm call frequency was measured as the number of 1-h audio files in which leopard alarm calls occurred.

We checked all photographs at the sleeping site ( $N = 96\,078$ ) for leopards and identified individuals based on unique spot patterns. If a leopard was

photographed twice in a given hour by the same or a different camera, it was considered one event. If the same leopard was photographed during more than one hour on a given night, each was considered a separate event. This happened on only one night when a female leopard was photographed over three hours as she returned to retrieve bushbuck (*Tragelaphus scriptus*) remains.

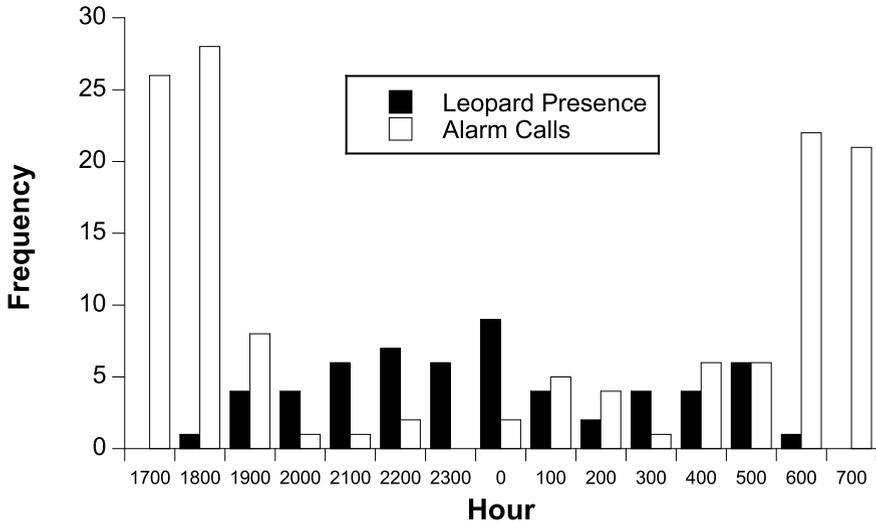
### 3. Results

#### 3.1. Leopard movements relative to leopard alarm calls

Vervets at the sleeping site gave leopard alarm calls during 133 of 4538 audio files (3%) spread out over 98 of 305 (32%) nights. Camera traps recorded 58 leopard events on 53 of 346 (15%) nights (one event occurred during the day). Spotted hyenas (*Crocuta crocuta*) were also photographed, but although vervets elsewhere can give leopard alarm calls to them (Seyfarth et al., 1980b), we have never heard the vervets at our study site alarm-call to them. Other carnivores that also sometimes elicit leopard alarm calls from vervets, i.e., lions, cheetahs and servals (Seyfarth et al., 1980b; Enstam & Isbell, 2002), were not photographed. The total number of nights differs for acoustic recordings and camera traps because they became operational on different dates and the acoustic recorder sometimes failed.

Combined data from camera trap images and vervets' leopard alarm calls indicate that leopards were nearby on a minimum of 36% (124/346) of all nights. It is a minimum estimate because leopards did not always walk in front of the cameras. Sometimes we found leopard footprints in the mornings although there were no photographs of leopards the night before, and sometimes the collared leopards were not photographed when they were at the sleeping site.

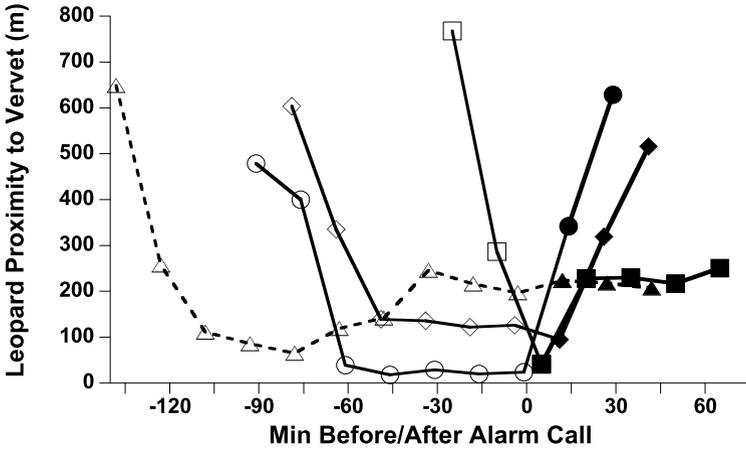
Audio files are available for the hours in which 57 of the 58 nocturnal camera trap leopard events occurred. Together, the camera trap leopard events and leopard alarm calls were distributed across all hours of the 15-h diel sampling period, indicating that leopards could be near the sleeping site during any of those hours (Figure 1). However, leopard alarm calls peaked around dusk and dawn whereas leopard presence in the camera traps peaked at midnight (Figure 1). There was a significant negative correlation between leopard alarm calls and leopard presence in the camera traps (Spearman rank correlation,  $r_s = -0.70$ ,  $p = 0.004$ ,  $N = 15$ , 2-tailed). These data suggest



**Figure 1.** Number of 1-h audio files during which vervets gave leopard alarm calls in a given hour during the sampling period vs. number of times in a given hour in which camera traps photographed leopards at the sleeping site.  $N$ , audio files per h = 298–305.

that leopards stayed farther away from the sleeping site when vervets gave alarm calls.

Data from the two collared leopards that used the sleeping site confirmed that leopards avoided coming closer after vervets gave leopard alarm calls, and revealed that they actively moved away to at least 200 m. Collared leopards approached the sleeping site on nine nights, and the recorder functioned on eight of those nights. Vervets gave leopard alarm calls on four of the eight nights. On the three nights when leopards were less than 200 m from the collared vervets at the initiation of alarm-calling, based on the timing of the next GPS fix, they moved at least 200 m from the vervets no later than 14–26 min after the alarm calls began. On the fourth night, the leopard remained in place when the vervets began alarm-calling. Although the collared vervets were as close as 65 m to the leopard at one point, they only alarm-called after moving over 200 m away 1.5 h later, suggesting they had not seen the leopard when they were closer to it (Figure 2). The leopards also changed their direction of movement on the three nights when they moved away (Figure 3), whereas they moved continually forward following the river on the four nights without alarm calls from vervets (Figure 4).

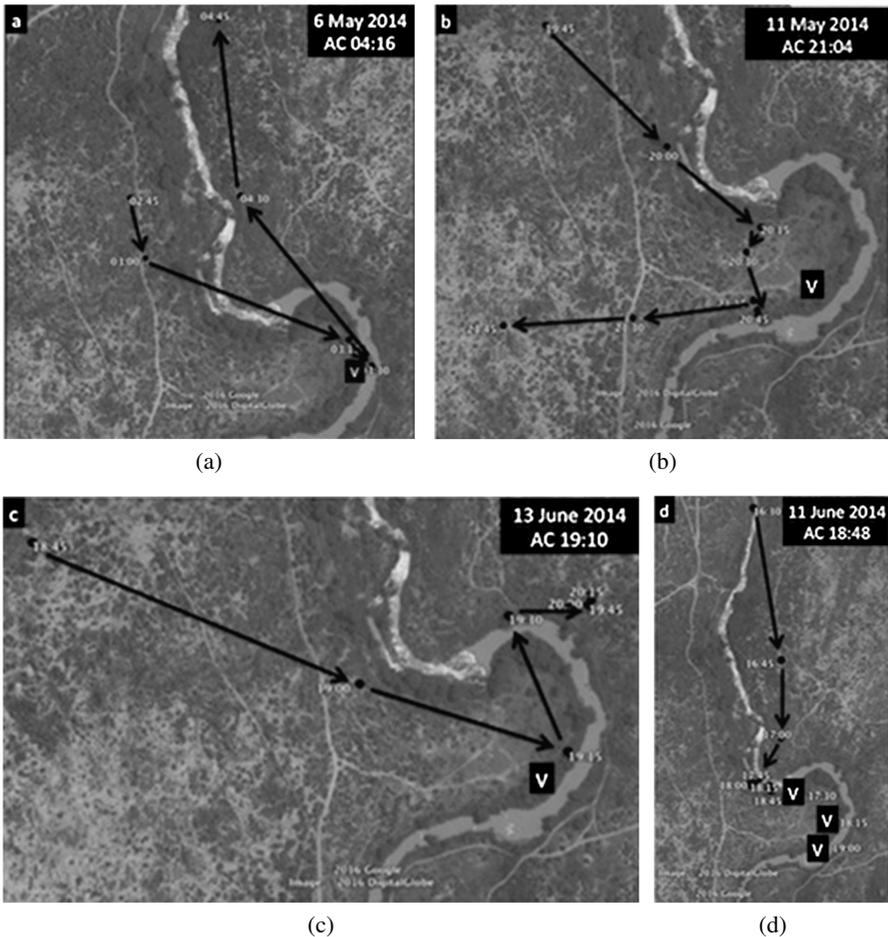


**Figure 2.** Proximity of collared leopards to collared vervets on the three nights when the leopards approached the vervets’ sleeping site, and on the one evening when vervets approached the leopard, before and after vervets gave alarm calls. Open symbols = proximity before alarm calls began; solid symbols = proximity after alarm calls began. Solid lines = nights leopard moved away >200 m from vervets after alarm calls; dashed line = night vervets moved >200 m away from leopard before giving alarm calls. Distance between consecutive symbols reflects speed of travel.

3.2. Leopard movements relative to human presence

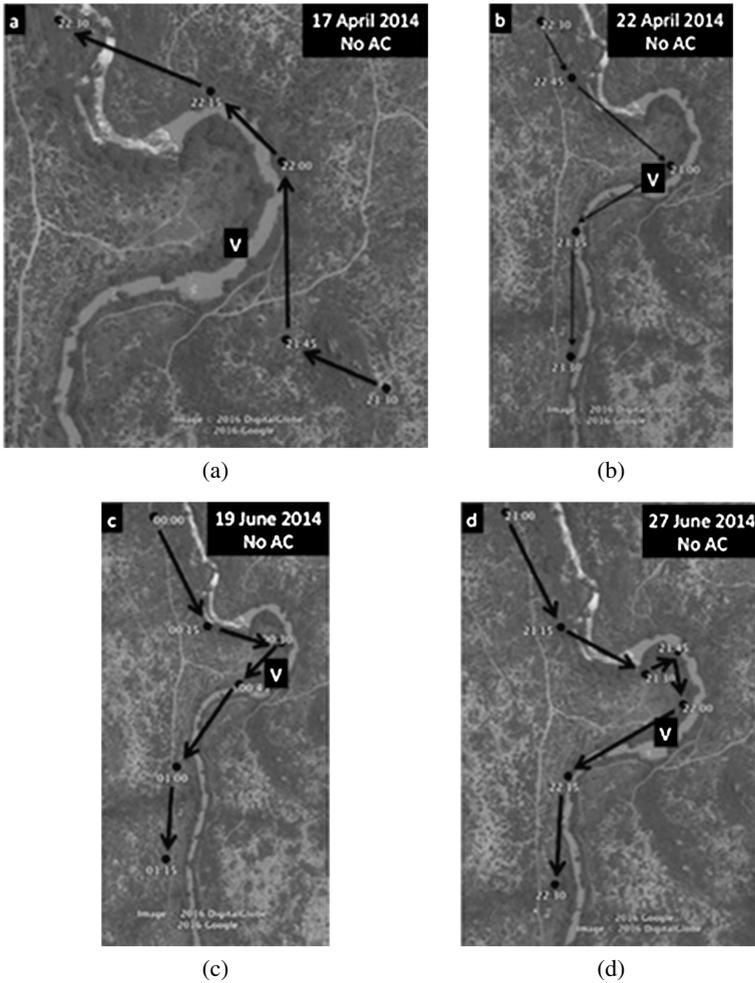
Because we were present at the sleeping site regularly around dawn to census the vervets and dusk to download GPS data, we examined the possibility that leopard avoidance of the sleeping site at dusk and dawn was due to avoidance of humans instead of a response to vervet alarm calls. If leopards were avoiding humans, we would expect them to move away upon our approach. Using camera trap photos of 598 arrivals/departures of humans between 17:00 and 08:00, the majority by vehicle, we found, not surprisingly, that hours in the diel cycle when leopards were caught on camera at the sleeping site were negatively correlated with hours in the diel cycle when humans arrived there (Spearman rank correlation:  $r_s = -0.60$ ,  $p = 0.009$ ,  $N = 15$ , 1-tailed).

This correlation does not appear to be causal, however. Leopard movements before and after humans approached to within 200 m (corresponding to just below the apparent threshold distance of leopard movements in response to vervet alarm calls) were known for 16 encounters at the sleeping site and throughout the collared leopards’ home ranges. Mean  $\pm$  SD net displacement of leopards ( $45.5 \pm 16.0$  m,  $N = 16$ ) 15 min after humans’ closest



**Figure 3.** Leopard movements on nights when vervets gave alarm calls. AC (top right), time of first alarm call; solid circles, location of leopard at 15-min intervals; V, location of collared vervet.

approach was much smaller than that of humans ( $1308.2 \pm 232.9$  m,  $N = 16$ ; Wilcoxon signed-ranks:  $W = -136$ ,  $p = 0.0005$ , 2-tailed), indicating that humans were the ones who departed while leopards remained in place or nearby. In one event at the sleeping site, a collared but unseen leopard actually approached us before leaving. We also observed leopards at the sleeping site on 10 occasions. In nine observations, the leopard either slowly walked away or sat and watched us before walking away. In the tenth, olive baboons



**Figure 4.** Leopard movements on nights when vervets did not give alarm calls. No AC (top right), no alarm calls; solid circles, location of leopard at 15-min intervals; V, location of collared vervet.

(*Papio anubis*) chased the leopard away. In sum, there was no evidence that leopards avoided humans to the extent that they confounded our results.

#### 4. Discussion

Multiple technologies were required to detect the dynamic, mutually responsive nature of the predator–prey relationship between leopards and vervets.

Using camera traps, acoustic recorders and GPS units, we found that leopards were responsive to alarm calls given by vervets. They approached more closely when the vervets did not alarm-call, and if they were less than 200 m away when alarm-calling began, within minutes they moved at least that far away. Thus, in addition to alerting conspecifics to the presence of leopards (Struhsaker, 1967; Seyfarth et al., 1980a, b), vervet leopard alarm calls function as a predator deterrent, as has been suggested for the alarm calls to leopards produced by several other primate species (Zuberbühler et al., 1997, 1999; Schel et al., 2010). Leopards likely move on partly because the alarm calls will have also alerted animals of other species to their presence, making hunting more difficult (e.g., Lea et al., 2008; Müller & Manser, 2008; Kitchen et al., 2010).

Leopards are thought to be the deadliest predator of Old World monkeys (Isbell, 1990, 1994; Cowlshaw, 1994; Cheney et al., 2004; Hart & Sussman, 2005; Isbell et al., 2009). This study is the first to provide a quantitative estimate of the frequency with which leopards approach vervets at night. Whether the frequency of approaches by leopards near primates at our study site (minimally 36% of all nights) is unusual or the norm will require similar studies elsewhere. It is possible that it is unusually high because the number of leopards using the area around the sleeping site was higher than is typical (Chase Grey et al., 2013). Normally little home range overlap occurs between individual leopards of the same sex (Bailey, 1993; but see Kiffner et al., 2012), but we identified at least three adult females and three adult males at the sleeping site.

We were not able to monitor all leopards or alternative prey species that may have affected leopard movement near the sleeping site, but do not expect such factors would have deterred leopards from the site in the stark temporal patterns found in this study.

We also found no support for the alternative that leopards avoided the sleeping site at dusk and dawn because of human presence. Leopards in the study area did not flee from humans who approached by vehicle or on foot, and so were not particularly averse to human presence. The study site has hosted researchers, herders, and research station and ranch employees for many years, and leopards have likely adjusted to local human activity to some degree. In some parts of the world, leopards even thrive near urban areas and yet they remain elusive and infrequently seen (Athreya et al., 2013; Odden et al., 2014). Flexible behaviour that allows them to live near humans

may include avoiding hunting while humans are present and becoming more active when people are more inactive (Busse, 1980; Isbell & Young, 1993; Ngoprasert et al., 2007; Odden et al., 2014).

Our findings have cautionary implications for prey-focused studies of behavioural predator–prey interactions. Recent studies have attempted to improve on estimates of predation risk by examining where alarm calls are given within the home range, the assumption being that a higher frequency of alarm calls indicates greater risk (Willems & Hill, 2009; Coleman & Hill, 2013; Campos & Fedigan, 2014). Our study shows, however, that alarm calls keep leopards away. Thus, applying the argument from these recent studies to our data would lead to the illogical conclusion that vervets are at greater risk when leopards are farther away. In fact, risk is likely to be greater when vervets do not give alarm calls to a leopard that is nearby because they will have not yet detected the leopard. Our data suggest that although alarm calls may be good indicators of leopard presence, they are not necessarily good indicators of risk, because they are a predator deterrent.

Such studies expose the limitations of focusing on only one player in predator–prey interactions. The importance of studying the behaviour of predators and prey simultaneously cannot be underestimated if the goal is to fully understand their undoubtedly dynamic interactions (Lima, 2002). Now that remote technologies are readily available to facilitate simultaneous study, greater opportunity exists to expand our knowledge of predator–prey relationships.

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