No evidence of reactive avoidance of baboons (*Papio ursinus and Papio anubis*) to the presence of predators

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Abstract

Predators exert strong selective pressure on prey species, shaping their behavioral adaptations. Prey species use proactive responses, such as site selection and the adjustment of daily activity patterns to anticipate and avoid predation exposure. In contrast, reactive responses, including fleeing, referential signaling and retaliation, occur after encountering a predator to mitigate the immediate predation risk. The presence of a predator in an area can also generate longer-term responses such as reactive avoidance, defined here as the temporary avoidance of the area following the passage of a predator. Such a long-term reactive response remains understudied in primates. To investigate reactive avoidance, we analyzed an extensive camera trap dataset of more than 3,000 detections of both chacma (*Papio ursinus*) and olive (*Papio anubis*) baboons, including almost 7,000 detections of their main predators, lions (*Panthera leo*), leopards (*Panthera pardus*) and spotted hyenas (*Crocuta crocuta*), in four savanna sites (Madikwe Game Reserve, Tswalu Kalahari Private Wildlife Reserve and the Associated Private Nature Reserves, South Africa; Serengeti National Park, Tanzania). We examined whether baboons display species-specific reactive avoidance towards predators up to 72 hours after the detection of a predator using randomization tests. We found no significant decrease in baboon presence (defined as the number of baboon detections) 0 to 24 hours, 24 to 48 hours and 48 to 72 hours after the detection of any predator species. These results suggest that baboons may not display reactive avoidance and rely on alternative predator-avoidance strategies, such as proactive avoidance or aggressive retaliation, to mitigate predation risk.

Keywords: anti-predator behavior, camera trap, leopard, lion, predator-prey interactions, primate, randomization test, spotted hyena, tropical ecosystem.

Introduction

Predation exerts a strong selective pressure on prey species due to its impact on individual fitness and survival (Humphries & Driver, 1967; Harvell, 1990; Krebs & Davies, 2009). Prey species have evolved a diverse range of behavioral responses to enhance their survival as they encounter fluctuating predation risk in their environment (Lima & Dill, 1990; Kie, 1999). Behavioural adaptations are inherently flexible and allow prey to modify the nature and intensity of their responses based on their spatial and temporal perception of risk in the surrounding environment (i.e., the landscape of fear, Laundré et al., 2001; Creel & Winnie, 2005; Palmer et al., 2022), and can be classified into proactive and reactive responses (Broekhuis et al., 2013; Courbin et al., 2016; Creel, 2018; Palmer & Packer, 2021; Say-Sallaz et al., 2023).

Proactive responses are behavioral adjustments made in anticipation of predation risk, based on prior knowledge of predator locations and preferred habitats (Creel et al & Christianson, 2008; Broekhuis et al., 2013; Creel et al., 2014). These adjustments, which result in the interaction with resource and refuge availability in the landscape (Willems & Russell, 2009; Suscke et al., 2021), operate over broad spatial and temporal scales such as home ranges and seasonal cycles (Droge et al., 2016). For example, orangutans (*Pongo spp*.) proactively select nest sites that provide greater camouflage, making it more difficult for predators to detect both them and their young (van Casteren, 2012). Hamadryas baboons (*Papio hamadryas*) make use of cliff faces (Schreier & Swedell, 2012) as sleeping and refuge sites to limit predator accessibility to the group and increase predator detectability (Anderson, 1999; Bidner et al., 2018). Chacma baboons (*Papio ursinus*) use refuge areas on the edge of urban environments, spending less than 1% of their time within the urban area, as a strategy to avoid human presence (Fehlmann et al., 2017). They also increase vigilance when away from roosting sites or when isolated from group members, enhancing threat detection in

vulnerable situations (Fischer et al., 2001). However, when foraging, the item size and complexity of the foraging task might reduce the level of vigilance of the individual (e.g., reduced vigilance when processing small food items requiring more attention, Allan et al., 2024).

Reactive responses, in contrast, are immediate reactions triggered by the detection of a predator (Broekhuis et al., 2013). These responses occur on smaller spatial and temporal scales such as foraging sites and across diel activity periods (Droge et al., 2016), driven by real-time threats. As a short term reactive response, white-faced capuchins (*Cebus capucinus*), vervet monkeys (*Chlorocebus pygerythrus*) and spectral tarsiers (*Tarsius tarsier*) commonly use referential signaling to alert other group members after the detection of a predator (Seyfarth et al., 1980; Fichtel et al., 2005; Gursky, 2007). Bonobos (*Pan paniscus*), colobine monkeys (*Colobus guereza*) and baboons (*Papio spp*.) seek refuge in elevated areas (e.g., tree canopies and cliffs) to reduce their vulnerability to terrestrial predators (Cowlishaw, 1994; Von Hippel, 1998; Isbell et al., 2018; Druelle et al., 2020). Chacma baboons also demonstrate aggressive predator mobbing when facing a predator, where the group collectively confronts and harasses the predator to deter the attack (Bailey, 1993; Cowlishaw, 1994; Jooste et al., 2013; Isbell et al., 2018). In addition to these short-term responses, some taxa also display long-term reactive avoidance, leaving the disturbed area for several hours to several days, as frequently observed in ungulates (e.g., in Burchell's zebra (*Equus quagga*), Courbin et al., 2016; in red deer (*Cervus elaphus*), Chassagneux et al., 2020). However, it remains unclear whether primates actively move away from sites visited recently by predators for extended periods of time (Allan et al., 2024; Hammond et al., 2025).

Baboons present an ideal study species to explore primate anti-predator behavior. As a prey species, baboons encounter a diverse range of predators due to their broad geographic distribution (Busse, 1980; Cowlishaw, 1994; Jooste et al., 2013; Isbell et al., 2018), such as

lions (*Panthera leo*), leopards (*Panthera pardus*) and spotted hyenas (*Crocuta crocuta*) (Busse, 1980; Jooste et al., 2013; Dröge et al., 2017; Isbell et al., 2018). Although baboons are usually not the main target for these predators (Busse, 1980; Jooste et al., 2013; Dröge et al., 2017; Isbell et al., 2018), they nevertheless contribute to significant baboon mortality (Busse, 1980; Cowlishaw, 1994). Leopards and lions are both ambush predator species, lions hunting baboons during the day, whereas leopards hunt during both diurnal and nocturnal periods, often targeting baboons at their roosting sites at night (Busse, 1980; Bidner et al., 2018; Isbell et al., 2018). Spotted hyenas are cursorial predators (Trinkel, 2010; Wentworth et al., 2011), which mostly target baboons when the opportunity arises as opposed to actively hunting them (Busse 1980; Cowlishaw, 1994; Trinkel, 2010; Wentworth et al., 2011). These different predation strategies are known to trigger different anti-predator responses in ungulate prey species (Berger, 1979; Palmer et al., 2021). Although species-specific responses among primates have been overlooked, there is emerging evidence of similar anti-predator responses occurring within this taxon (Gursky, 2007; Seiler et al., 2013; Adams & Kitchen, 2020). Suire et al. (2023) found that male olive baboons (*Papio anubis*) tend to position themselves at the periphery of the group to protect more vulnerable group members such as females and juveniles from cursorial predators.

So far, most studies on baboon-predator interactions have relied primarily on direct field observations (e.g., Busse, 1980; Hill & Weingrill, 2007; Allan et al., 2021). While these methods offer detailed insights into short-term reactive responses, they may influence animal behavior due to the presence of human observers (predator shelter hypothesis, Shannon et al., 2014). Additionally, they are often difficult to implement over extended periods or under specific conditions such as nighttime, limiting their usability to explore long-term reactive responses (Busse, 1980; Nowak et al., 2014; Dill & Frid, 2020; LaBarge et al., 2022; Allan et al., 2024). In contrast, camera traps are a non-invasive, uninterrupted monitoring alternative

(Newey et al., 2015), which proved to reliably detect large carnivores (Meek et al., 2016) as well as primates (Boyer-Ontl & Pruetz, 2014; Bersacola et al., 2022). Camera traps have largely been used to study predator-prey interactions (Smith et al., 2020), particularly space use (e.g., Cusack et al., 2017; Keim et al., 2019) and activity pattern overlaps (e.g., Linkie & Ridout, 2011; Foster et al., 2013). The widespread adoption of camera traps in recent decades has led to the development of long-term monitoring programs across extensive areas (Swanson et al., 2015; Blount et al., 2021), providing a new source of data for the study of predator-prey interactions (e.g., Hammond et al., 2025). Although promising, are these non-targeted, large-scale datasets adequate for examining long-term primate reactive responses to predators?

In this study, we took advantage of the largest camera trap-based monitoring project in Africa, Snapshot Safari (Swanson et al., 2015; Pardo et al., 2021) and analyzed 10,000 camera trap detections from three sites in South Africa and one site in Tanzania to test whether baboons exhibit species-specific reactive avoidance in response to the presence of predators. We tested three hypotheses related to the interaction between baboons and predator characteristics: H1) we expected baboon presence to decrease significantly 0 to 24 hours following the detection of spotted hyena, a terrestrial cursorial predator. Spotted hyenas only opportunistically hunt baboons (Busse, 1980; Cowlishaw, 1994; Trinkel, 2010; Wentworth et al., 2011) and are highly mobile across the landscape (Kolowski et al., 2007). As semi-arboreal primates, baboons predominantly forage in proximity to trees or cliffs (Schreier & Swedell, 2012; Fehlmann et al., 2017) that serve as potential refuges in the event of a predation attempt. We therefore predicted that baboons should be weakly influenced by the occurrence of spotted hyena, returning to the disturbed area shortly after the detection of spotted hyena. H2) we expected baboon presence to decrease significantly 0 to 48 hours following the detection of leopard, a semi-arboreal ambush predator. Leopards can pursue

baboons into trees, which may prompt the entire group to relocate for a longer period (Busse, 1980; Trinkel, 2010; Wentworth et al., 2011; Isbell et al., 2018). However, leopards are also highly mobile and may not remain in the same area for long periods (Martins and Harris, 2013; Hubel et al., 2018). We therefore predicted that baboons should be more strongly affected by leopard than spotted hyena presence, leading to their displacement from the disturbed area with a gradual return following the detection of leopard. H3) we expected baboon presence to decrease significantly 0 to 72 hours following the detection of lion, a terrestrial ambush predator. Although baboons can evade lion predation by retreating to elevated refuges, lions can exhibit limited daily displacement and may remain in the same area for extended periods (Elliot et al., 2014), potentially forcing baboons to relocate for a prolonged duration to maintain their normal activity patterns (particularly for foraging) in safer conditions. We therefore predicted that baboons should be most strongly affected by lion presence, resulting in the longest avoidance period compared to other predators, with a slow return following the detection of lion.

Methods

Study site selection and description

In this study, we exploited data from the ongoing camera trap monitoring project *Snapshot Safari*, which spans multiple sites and countries (Tanzania, data publicly available at Dryad: http://dx.doi.org/10.5061/dryad.5pt92, Swanson et al., 2015; South Africa, Pardo et al., 2021). Of the 32 sites surveyed, we included sites where all three target predators were detected along with baboons. The South African study sites included Madikwe Game Reserve (MAD, 24°49'S-26°13'E; Figure 1A), Tswalu Kalahari Private Wildlife Reserve (TSW, 27°14'S-22°23'E; Figure 1B), and the Associated Private Nature Reserves (APN, 24°20'S-31°20'E; Figure 1C), inhabited by chacma baboons (Stone et al., 2013). The Tanzanian study

site was Serengeti National Park (SER, 2°19'S-34°49'E; Figure 1D), occupied by olive baboons (Zinner et al., 2011). All four study sites were located within the savanna biome, characterized by open grasslands interspersed with isolated trees (Sankaran et al., 2005).

MAD is a 750 km² fenced game reserve located in the Northwest Province, on the border of South Africa and Botswana, within the central bushveld bioregion (Szott et al., 2020). The landscape is characterized by ridges and thorny woodlands dominated by acacia species (Szott et al., 2020). TSW, located in the Northern Cape Province, is a 1,020 km² fenced reserve in the Eastern Kalahari bioregion, with portions extending into the Kalahari dunefields. Elevation ranges from 1,020 m a.s.l. in lower-lying areas to 1,586 m a.s.l. at the highest point (Davis et al., 2010). The vegetation consists of discontinuous annual and perennial grasses interspersed with deep-rooted trees, such as the camel thorn (*Vachellia erioloba*, Beaumont & Bednarik, 2015). APN is a collective of five interconnected reserves (Timbavati, Thornybush, Klaserie, Balule, and Umbabat Private Nature Reserves) covering 1,800 km² in the mopaneveld bioregion of Limpopo and Mpumalanga provinces. It is open to Kruger National Park (Bedetti et al., 2020; Rutherford et al., 2006). The APN vegetation is highly variable, with isolated trees in a continuous grass understory interspersed with patches of dense woody vegetation (Scholes & Archer, 1997). The SER study site corresponds to an open sub-section of 1,125 km^2 inside the core of Serengeti National Park, Tanzania, part of the East African savanna biome. It is covered by grasslands interspersed with scattered trees, with steeper slopes to the North-West (Swanson et al., 2015).

Camera trap data

Data for MAD, TSW, and APN were collected between June 2017 and November 2019 (29 months), while data for SER were collected between June 2010 and May 2013 (35 months).

As is common in large-scale monitoring programs, camera traps (n = 357) from different brands (Cuddeback's Professional Series x-change, white flash in South Africa, and Scoutguard (SG565) incandescent cameras in SER) were deployed. Camera trap placement followed a systematic layout in MAD, TSW, and SER, where camera traps were positioned at the center of a 5 km² grid pattern. Camera trap placement in the APN followed a random allocation layout (*sensu* Meek et al., 2014), based on habitat and terrain structure. We removed five camera traps from the MAD dataset that were positioned specifically near waterholes, as predator-prey interactions may likely differ at waterholes due to the trade-off between the need for scarce resources (i.e., water) and predator avoidance (Edwards et al., 2016). In the present study, we used a total of 346 camera traps (nMAD = 40; nTSW = 31; nAPN = 56; nSER = 219) for our analyses (see below for data processing and selection steps).

The camera traps were enclosed in steel casings and fixed at a height of approximately 50 cm above the ground (Swanson et al., 2015; Pardo et al., 2021). To minimize glare caused by the rising and setting sun, the camera traps were oriented to face as far North or South as possible. Cameras were also directed based on vegetation cover, avoiding areas of high grass density to reduce the probability of obtaining blank pictures and maximizing animal detection. The sensitivity of each camera trap was set to a medium level (50-75%) to minimize false triggers caused by windblown vegetation. No lures were used to attract any species to the camera trap sites. Each camera trap was programmed to take three pictures for every motion detection during the day and one at night (see Pardo et al., 2021 for a more detailed description of the protocol in the South African sites; and Swanson et al., 2015 for the Tanzanian site). To minimize the impact of potential variability in detection probabilities due to differences between protocols and sites (Cusack et al., 2017; Herrera et al., 2021), we analyzed our four sites separately.

Species were identified in each capture event (i.e., any single picture or consecutive series of pictures initiated by an animal-trigger, regardless of the number of individuals present in the picture(s), Meek et al., 2014) using two methods: (i) for SER, the citizen science program Zooniverse (www.zooniverse.org) which uses classifications from the general public (consensus after 10 matching classifications of species or species combination; see details in Swanson et al., 2015); (ii) for the three South African sites, the online program TrapTagger (www.wildeyeconservation.org), which was used to manually record animal species as identified by trained laboratory technicians. After species classification, we obtained a total of n = 1,625 detections of chacma baboons, n = 1,531 detections of olive baboons, n = 6,929 detections of spotted hyenas, n = 449 detections of leopards and n = 3,886 detections of lions.

As our objective was to evaluate the presence of baboons up to 72 hours after (and symmetrically, before) the detection of a predator, we exclude any predator detection that occurred within the 72 hours following the camera's deployment and within 72 hours before the end of the camera's operational lifespan. To ensure consistency, we applied a 30-minute time-to-independence filter to predator detections, retaining the central detection within a cluster of consecutive detections as the main detection for a given predator detection. This threshold aligns with previous studies that showed that increasing the independence interval has minimal impact on observed activity patterns of large carnivores (Linkie & Ridout, 2011; Searle et al., 2021; Tjaden McClement et al., 2025). Retaining the central detection instead of the first detection as usually conducted in the literature ensures symmetry when testing for baboon response to a predator before and after the predator detection in our study design. Our final dataset was thus composed of n = 1,584 detections of chacma baboons, n = 1,458 detections of olive baboons, n = 5,071 detections of spotted hyenas, n = 355 detections of leopards and n = 1,532 detections of lions (Table 1).

Statistical analyses

To assess whether baboon presence after a predator detection was lower than expected by chance, we used a randomization test to compare the number of baboon detections after the predator detection to the ones obtained under the assumption of non-avoidance of predators (Niedballa et al., 2019; Zhang & Zhao, 2023). We calculated the total number of baboon detections following predator detections in each site, for each predator species independently. This was done for three consecutive 24-hour time-blocks after predator detection: 0 to 24 hours after the predator detection, 24 to 48 hours after the predator detection and 48 to 72 after the predator detection. Extending the observation period beyond 72 hours after predator detection was avoided due to the difficulty in associating the prey species presence or absence with the original predator detection (Courbin et al., 2016; Swinkels et al., 2023). We further analyzed baboon detections before the predation detection to establish a baseline for their presence, with the expectation of no significant difference in the number of baboon detections. This allowed us to determine the strength of the predator effect while accounting for natural fluctuations in baboon activity. The analysis of baboon detections before a predator detection was also conducted in three 24-hour time-blocks over a 72-hour period.

Predator species have been reported to sometimes follow each other (e.g., for kleptoparasitism, Cusack et al., 2017). In our dataset, < 5% of the days when a predator was detected at a camera trap site were also characterized by the detection of a second predator species (0.7% in MAD, 0.0% in TSW, 2.5% in APN, 3.6% in SER). We thus considered that there was no significant risk of interpreting baboon reactive avoidance due to a predator species when examining the effect of another species.

To obtain the distribution of baboon detections under the null hypothesis (i.e., non-avoidance of predators), we randomized the dates while preserving the original timing to

maintain natural diel activity patterns of each predator detection 1,000 times in each camera trap-roll (i.e., the continuous working time of a camera trap between two services, approximately three months) detecting both baboons and the predator of interest. We then estimated, for each randomized data set, the total number of baboon detections in each time-block. We excluded any camera trap with a lifespan < 30 consecutive days to avoid restricting the randomization process. Predator detections captured by camera traps with a shorter lifespan could only be randomized within a limited time window, which would produce unreliable results.

For each 24-hour time-block, we evaluated whether the observed number of baboon detections deviated significantly from the assumption of non-avoidance of predators. To do so, we calculated the significance value (*p*) for each time-block as the proportion of iterations in our randomization procedure in which the number of baboon detections was inferior (superior, respectively) or equal to the observed number of baboon detections after (before, respectively) the predator detection. All data processing and analyses were performed using the R software (version 4.5.1; R Core Development Team, 2025).

Validation of the randomization approach

To validate our randomization approach, we tested it on Burchell's zebras (*Equus quagga)*. Burchell's zebras are known to display reactive avoidance in response to lions for up to 24 hours after an encounter (Thaker et al., 2011; Courbin et al., 2016; Say-Sallaz et al., 2023), therefore we expected to find a significant response in the 0 to 24 hour time-block, after lion detection.

APN had the highest number of lion detections among the South African sites (n_{APN} = 188, n_{MAD} = 17, n_{TSW} = 51; sample sizes after data selection process). Although SER had higher numbers of both lions (n_{SER} = 1,276) and Burchell's zebras (n_{SER} = 60,212), analysing

these data revealed too computationally intensive using our randomization procedure. Additionally, the number of Burchell's zebras (n_{APN} = 2,047) was of the same magnitude as the number of baboons in SER, which represents our largest dataset in terms of baboon detections (n_{SER} = 1,458), making it a suitable comparison point to assess the effect of sample size on the results.

To assess the effect of sample size on the analyses, we performed 100 random subsets of Burchell's zebra detections in APN to match the number of baboon detections (n_{APN} = 500). We thus created a down sampled data set, for which we conducted the randomization analysis for each of the 100 iterations and calculated the frequency of significant versus non-significant values.

Results

Method validation: reactive avoidance in Burchell's zebras

As expected, Burchell's zebras showed significant reactive avoidance 0 to 24 hours after lion detection in APN (p = 0.024, Figure 2), providing support for the soundness of our randomization approach. We did not find significant reactive avoidance 24 to 48 hours (p = 0.176) and 48 to 72 hours (p = 0.495) after lion detection (Table 2). After taking a subset of Burchell's zebra detections to match the number of baboon detections in APN (n = 500), we could no longer detect this response 0 to 24 hours following lion detection (p *(mean ± SD)* = 0.182 ± 0.103, Supplementary Figure 1).

Reactive avoidance in baboons

Our results did not show any significant reactive avoidance in baboons in response to the detection of spotted hyenas, across any time-block after predator detection (0 to 24, 24 to 48, or 48 to 72 hours) in any of the three study sites in South Africa (all p > 0.05, Table 2, Figure

3). Similarly, there was no evidence of baboons displaying reactive avoidance following the detection of lions or leopards in any South African site and across any time-block after their detection (all $p > 0.05$, Table 2, Figure 3). However, in APN, baboon presence increased significantly 48 to 24 hours before the detection of lions ($p < 0.001$) and 24 to 0 hours before the detection of spotted hyenas ($p < 0.007$, Table 2, Figure 3). In TSW, baboon presence increased significantly 24 to 0 hours before the detection of lions ($p = 0.033$, Table 2, Figure 3).

In SER, where the number of baboon detections exceeded those at all South African sites (SER detection rate approximately 4.21 times higher than MAD, 2.92 times higher than APN and 1.98 times higher than TSW, Table 1), and was close to the number of Burchell's zebra detections in APN, we still did not detect significant reactive avoidance of baboons in response to any predator tested and across all time-blocks after predator detection (all $p > 0.05$, Table 2, Figure 3). Consistent with observations in APN, baboon detections in SER were significantly higher than expected under the null hypothesis 24 to 0 hours before the detection of spotted hyenas ($p < 0.008$, Table 2, Figure 3). Additionally, baboon detections in SER were significantly higher than expected under the null hypothesis 24 to 0 hours before the detection of leopards ($p = 0.012$, Table 2, Figure 3).

Discussion

Using camera trap data from a large-scale monitoring program in four different savanna sites in South Africa and Tanzania, we found no evidence that either chacma or olive baboons display reactive avoidance for as long as 72 hours after the detection of any of their main predators (lions, leopards and spotted hyenas). Contrary to our expectations, there was no detectable difference in the duration of the reactive avoidance response of baboons

according to predator characteristics (i.e., predator hunting strategy, predator daily mobility, predator specialization in baboon hunting) at such a time scale.

The absence of reactive avoidance at a one-to-three-day timescale suggests that baboons might rely on short-term rather than long-term anti-predator responses. Baboons usually forage in areas with tall trees which can serve as refuge against terrestrial predators such as lions and spotted hyenas (Cowlishaw, 1997). They also exhibit effective sentinel behaviors, one individual monitoring for threats while the rest of the group forages (Horrocks et al., 1986; Bezerra et al., 2008), which leads to the early detection of predation attempts. The danger is rapidly signaled to conspecifics via contact barks (Bailey, 1993; Cowlishaw, 1994; Jooste et al., 2013; Isbell et al., 2018), which allows for their prompt retreat. Baboons may thus remain in the vicinity of a predator, and retreat into refuges temporarily only in the instance of a predation attempt, rather than completely avoiding a potentially resource rich area for several days when frequented by a predator. Similarly, Hammond et al. (2025) found no evidence of predator-occupied area avoidance by chacma baboons and suggest that they might instead display short-term reactive avoidance. The modulation of reactive anti-predator responses by environmental variables such as the proximity of refuge areas reducing the vulnerability to predators has also been documented in other species (e.g., in woodchucks (*Marmota monax*), Kramer & Bonenfant, 1997; in European hares (*Lepus europaeus*), Weterings et al., 2016).

Additionally, baboons are notorious for their aggressive retaliation toward predators, particularly leopards (Buse, 1980; Bailey, 1993; Cowlishaw, 1994; Hayward et al., 2006: Jooste et al., 2013; Isbell et al., 2018). A review by Cowlishaw (1994) showed that, when baboons retaliate, they successfully deter predation in 93% of cases, and four out of 11 observed predation attempts resulted in the death of the attacking leopard. This behavior is predominantly exhibited by male in both chacma (Cowlishaw, 1994; Isbell et al., 2018) and

olive (MacCormick et al., 2012) baboons, owing to their larger teeth and body size (Virgadamo et al., 1972; Galbany et al., 2015; Johnson, 2003). Similarly, a large number of primate species, mainly males, display mobbing and counter-attack behavior as an anti-predator response (Schaik et al., 2022). Such a response could decrease predation attempts by lowering the predator's chance of successful capture and thus, their interest in the species (Lima & Dill, 1990; Cowlishaw, 1994; Alberts, 2018; Isbell et al., 2018). Therefore, predators could be perceived as less of a threat by baboons which would consequently be less inclined to avoid the area, even if frequented by predators.

Surprisingly, we detected evidence suggesting an increased presence of baboons before a predator detection across all study sites (except MAD). Although these results might be artifacts due to small sample sizes, they might also be related to the fact that baboons use the ground more frequently in the absence of predators as it is perceived as safer (Hammond et al., 2022; Hammond et al., 2025). This could lead to an increased capture rate of the same individuals during their terrestrial displacements in the monitored area. Although most primates primarily forage in trees, they may adopt more terrestrial foraging behaviors during periods when food resources are less abundant and require supplementation with grasses or other ground-based food items (e.g., Li, 2007), particularly baboons.

The ability to detect spatio-temporal avoidance confidently when applying a randomization procedure to camera trap data depends on the strength of the avoidance behavior and the number of detections of both species, the latter needing to be as high as 100 detections per species in the case of weak avoidance (Niedballa et al. 2019). In our method validation, we found that Burchell's zebras showed reactive avoidance toward lions within the 0 to 24 hour time-block after a lion detection, consistent with previous findings in this species (Thaker et al., 2011; Courbin et al., 2016; Say-Sallaz et al., 2023) and thus supporting the validity of our approach. However, after the number of detections of Burchell's zebras

was sub-sampled to match the highest number of baboon detections, we no longer detected reactive avoidance. Sample sizes being relatively low in our four study sites (particularly in MAD and TSW), we might lack statistical power to detect significant reactive avoidance in baboons. To completely rule out this possibility, more camera traps may be necessary to obtain better detection rates of both prey and predators. Si et al. (2014) and Evans et al. (2019) showed that when studying coyotes, adding one camera trap at each capture site increases the detection probability by four. Additionally, baboons being semi-arboreal, a mixed design of terrestrial and arboreal camera traps could be adopted to cover all three spatial dimensions of baboon movement and increase their detection rate (Bersacola et al., 2022). Although large-scale camera-trap based monitoring programs present a novel opportunity for preliminary explorations of predator-prey interactions, optimizing camera trap density and placement appears essential to improve detection rates, particularly for low density species with complex habitat use such as primates.

Conclusion

This study contributes to broadening our understanding of predator-prey interactions in two primate species. The potential absence of reactive avoidance in chacma and olive baboons raises important questions about the variability of their anti-predator strategies, not only in savanna biomes but also across other environments in response to different predators (Zinner et al., 2011; Stone et al., 2013). This study further highlights the influence of detection rates on the detectability of behavioral responses when using camera traps, as illustrated by the loss of significance of reactive avoidance in Burchell's zebras after the reduction of sample size. These limitations related to camera trap density and placement further emphasize the challenges of accurately quantifying prey-predator interactions among

semi-arboreal and low-density species using systematic and random layouts, common in large-scale monitoring projects.

Authors' contributions

Conceptualization: VR, FP – Methodology: NVR, LT, VR, FP – Data acquisition: HF, JV – Formal analysis: NVR, LT, VR, FP – Investigation: NVR, VR, FP, LT – Writing: Original draft: NVR, VR, FP, LT – Writing: Review & Editing: NVR, LT, VR, FP, HF, JV – Supervision: VR, FP – Funding acquisition: VR, JV

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Inclusion and diversity statement

The authors are committed to fostering an environment of open dialogue, respect, and cultural inclusion. Our collaboration between African and European researchers reflects our dedication to international scientific exchange and diverse perspectives. Within our research team and laboratory, we actively promote a supportive and inclusive environment. Our first author lives with temporal lobe epilepsy, a condition that affects both memory and language. We acknowledge the unique challenges this presents in research and take meaningful steps to ensure that our team remains understanding and accommodating to this disability. We firmly oppose all forms of discrimination based on sex, gender, race, or any other identity marker. Our partnership is grounded in fairness and merit, and we evaluate all contributions based on the quality and impact of the work, not on the individual's background or identity.

Data availability statement

Pictures from the Snapshot South Africa program can be requested at Snapshot Safari upon reasonable request. Pictures from the Snapshot Serengeti program are available from the Labeled Image Library of Alexandria – Biology and Conservation: http://lila.science/datasets/snapshot-serengeti. All classification data and metadata are publicly available at Dryad: http://dx.doi.org/10.5061/dryad.5pt92.

Code availability statement

The code to analyze and reproduce this study has been deposited in Zenodo and is available online at https://zenodo.org/records/15018760.

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Tables

Table 1. Number of detections for the species of interest: chacma baboon (*Papio ursinus*), olive baboon (*Papio anubis*), Burchell's zebra (*Equus quagga*), spotted hyena (*Crocuta crocuta*), leopard (*Panthera pardus*), and lion (*Panthera leo*), in Associated Private Nature Reserves (APN), Madikwe Game Reserve (MAD), Tswalu Kalahari Private Wildlife Reserve (TSW) (South Africa, data collected between 2017 and 2019), and Serengeti National Park (SER) (Tanzania, data collected between 2011 and 2013). A 30-minute time-to-independence filter was applied to predator detections (see Methods section for details).

Species	**Scientific name**	**Number of detections in MAD**	**Number of detections in TSW**	**Number of detections in APN**	**Number of detections in SER**
Lion	*Panthera leo*	17	51	188	1,276
Leopard	*Panthera pardus*	28	8	159	160
Spotted hyena	*Crocuta crocuta*	110	9	1,570	3,382
Chacma baboon	*Papio ursinus*	346	738	500	0
Olive baboon	*Papio anubis*	0	0	0	1,458
Burchell's zebra	*Equus quagga*	3,602	1,394	2,047	60,212

Table 2. Significance values (*p*) calculated by comparing the observed number of detections of chacma baboon (*Papio ursinus*) and olive baboon (*Papio anubis*) before and after predator detections: spotted hyena (*Crocuta crocuta*), leopard (*Panthera pardus*), and lion (*Panthera leo*), to the distribution of number of detections produced by randomizing predator detections under the assumption of non-avoidance, across six consecutive 24-hour time-blocks relative to the predator detection (72 to 48 hours before, 48 to 24 hours before, 24 to 0 hours before, 0 to 24 hours after, 24 to 48 hours after, 48 to 72 hours after) in the four study sites: Associated Private Nature Reserves (APN), Madikwe Game Reserve (MAD), Tswalu Kalahari Private Wildlife Reserve (TSW) (South Africa, data collected between 2017 and 2019), and Serengeti National Park (SER) (Tanzania, data collected between 2011 and 2013).

Study site	**Prey species**	**Predator species**	**-72 to -48 hours**	**-48 to -24 hours**	**-24 to 0 hours**	**0 to 24 hours**	**24 to 48 hours**	**48 to 72 hours**
MAD	Chacma baboon	Lion	0.503	1.000	1.000	0.900	0.469	0.452
		Leopard	1.000	0.105	1.000	0.808	0.802	0.496
		Spotted hyena	0.877	1.000	0.904	0.742	0.251	0.107
TSW	Chacma baboon	Lion	0.451	0.288	0.033 *	0.925	0.664	0.354
		Leopard	1.000	1.000	0.149	0.792	0.647	0.773
		Spotted hyena	1.000	1.000	1.000	0.912	0.714	0.722
APN	Chacma baboon	Lion	0.671	0.001 *	1.000	0.526	0.251	0.373
		Leopard	0.547	0.739	0.597	0.573	0.114	0.600
		Spotted hyena	0.886	0.072	0.007 *	0.225	0.498	0.144
SER	Olive Baboon	Lion	0.869	0.781	0.160	0.098	0.460	0.679
		Leopard	0.551	0.434	0.012 *	0.599	0.141	0.788
		Spotted hyena	0.574	0.317	0.008 *	0.984	0.400	1.000

* Significance to the level alpha = 0.05.

Figure captions

Figure 1. Map of the four study sites in South Africa (data collected between 2017 and 2019) and Tanzania (data collected between 2011 and 2013). A) Madikwe Private Game Reserve (MAD; n = 40 camera traps); B) Serengeti National Park (SER; n = 219 camera traps); C) Tswalu Kalahari Game Reserve (TSW; n = 31 camera traps); D) Associated Private Nature Reserves (APN; n = 56 camera traps). The green boundaries represent the borders of the study areas, the red circles represent the camera trap locations, with their assigned code printed above. Chacma baboon (*Papio ursinus*) occurs in the three South African sites, olive baboon (*Papio anubis*) occurs in the Tanzanian site.

Figure 2. Distribution of Burchell's zebra (*Equus quagga*) detections obtained from the randomized datasets (n = 1,000) before and after lion (*Panthera leo*) detection in Associated Private Nature Reserves (APN), South Africa (data collected between 2017 and 2019). Each panel corresponds to one of six consecutive 24-hour time-blocks relative to the predator detection: 72 to 48 hours before, 48 to 24 hours before, 24 to 0 hours before, 0 to 24 hours after, 24 to 48 hours after, 48 to 72 hours after. The red vertical lines represent the observed number of Burchell's zebra detections for each time-block. The shaded area corresponds to the density of randomization trials, the area under the curve thus being equal to 1. *: significance to the level alpha = 0.05.

Figure 3. Distribution of baboon (*Papio ursinus* and *Papio anubis*) detections obtained from the randomized datasets (n = 1,000) before and after predator detection: spotted hyena (*Crocuta crocuta*), leopard (*Panther pardus*), and lion (*Panthera leo*), across the four study sites: Associated Private Nature Reserves (APN), Madikwe Game Reserve (MAD), Tswalu Kalahari Private Wildlife Reserve (TSW) (South Africa, data collected between 2017 and

2019), and Serengeti National Park (SER) (Tanzania, data collected between 2011 and 2013). Each panel corresponds to one of the six consecutive 24-hour time-blocks relative to the predator detection: 72 to 48 hours before, 48 to 24 hours before, 24 to 0 hours before, 0 to 24 hours after, 24 to 48 hours after, 48 to 72 hours after. The red vertical line represents the observed number of baboon detections for each site/predator/time-block combination. The shaded area corresponds to the density of randomization trials, the area under the curve thus being equal to 1. *: significance to the level alpha = 0.05.

Figures

Figure 1

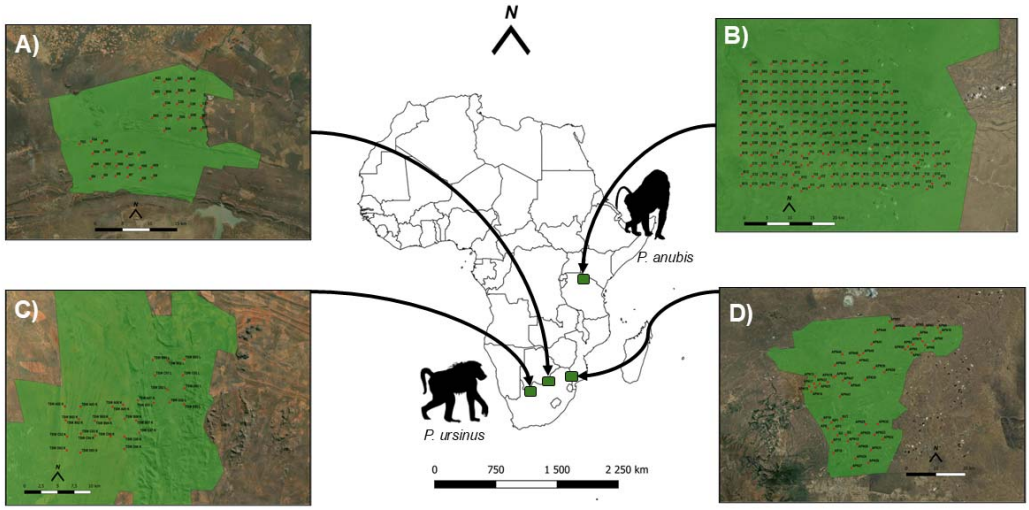


Figure 2

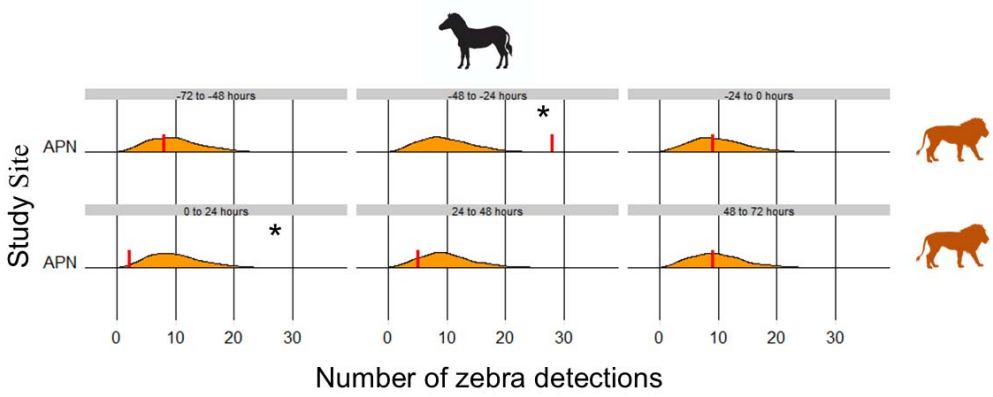
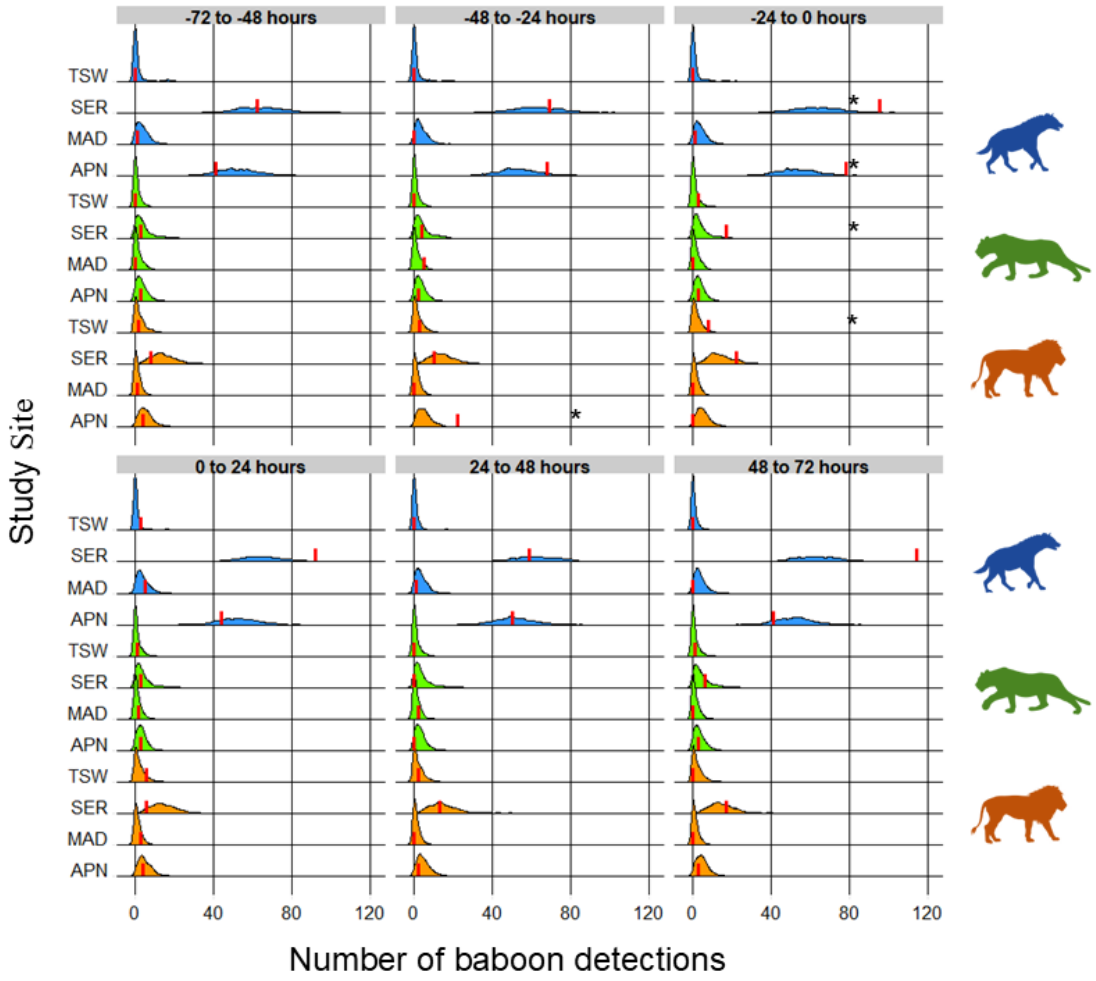
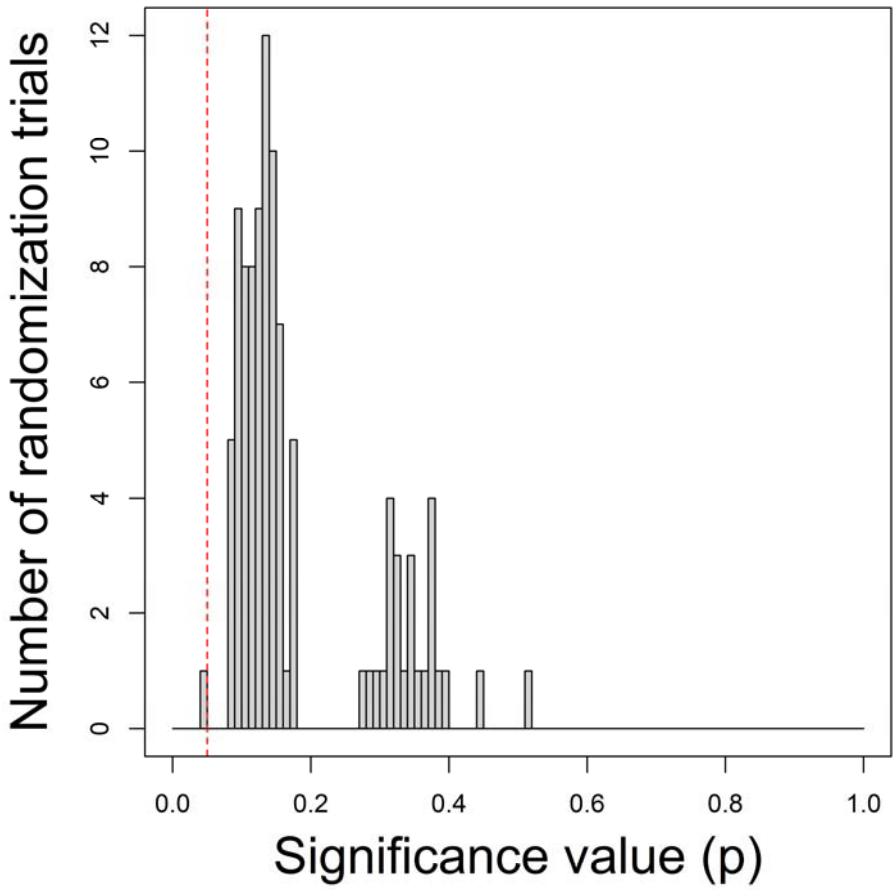


Figure 3


-72 to -48 hours
-48 to -24 hours
-24 to 0 hours
0 to 24 hours
24 to 48 hours
48 to 72 hours
TSW
SER
MAD
APN
Study Site
0
40
80
120
Number of baboon detections

Supplementary material

Supplementary Figure 1. Distribution of significance values (*p*) from the randomization test assessing the effect of lions (*Panthera leo*) on Burchell's zebra (*Equus quagga*) detections in Associated Private Nature Reserves (APN), South Africa (data collected between 2017 and 2019) within the 0 to 24 hours following lion detection. The test was conducted on randomly down-sampled Burchell's zebra detections datasets (n = 100). The red dashed line indicates the significance value threshold of alpha = 0.05, marking the significance level for detecting deviations from the assumption of non-avoidance.