# Absence of reactive temporal response of baboons to the occurrence of predators.

N. van Rooyen[1,2,] *, L. Thel[3,] *, J.A. Venter[3], H. Fritz[1,2], F. Prugnolle[1,2,#], V. Rougeron[1,2,#]

**Affiliations**

[1] International Research Laboratory, REHABS, CNRS-NMU-UCBL, George Campus, Nelson Mandela University, Madiba drive, 6529 George, South Africa

[2] Sustainability Research Unit, George Campus, Nelson Mandela University, George Campus, Madiba drive, 6529 George, South Africa

[3] Department of Conservation Management, Faculty of Science, Nelson Mandela University, George Campus, George, South Africa

*** Co-first authors:** N. van Rooyen[1,2,] *, L. Thel[3,] *

[#] **Co-supervised the work:** F. Prugnolle[1,2,] V. Rougeron[1,2,#]

**Corresponding authors:**

Rougeron Virginie, International Research Laboratory, REHABS, CNRS-NMU-UCBL, Sustainability Research Unit, George Campus, Nelson Mandela University, George, South Africa, rougeron.virginie@gmail.com/virginie.rougeron@cnrs.fr;

Nicholas van Rooyen, Department of conservation management, faculty of science, Nelson Mandela University George Campus, Nelson Mandela University, George, South Africa, s216653207@mandela.ac.za

# Abstract

Predation exerts a strong selective pressure on prey species, shaping their behavioral adaptations. While proactive strategies such as habitat selection and increased vigilance allow prey to anticipate threats, reactive responses, including immediate flight or retaliation, occur on direct detection of a predator. Baboons (*Papio spp.*) encounter various predators across their extensive range, but their behavioral responses to these threats remain poorly understood. Using camera trap data from four savanna sites—three in South Africa (Madikwe Game Reserve, Tswalu Kalahari Private Wildlife Reserve, and the Associated Private Nature Reserves) and one in Tanzania (Serengeti National Park)—this study examined whether chacma (*P. ursinus*) and olive (*P. anubis*) baboons exhibit reactive temporal avoidance following the occurrence of their main predators, lions (*Panthera leo*), leopards (*Panthera pardus*), and spotted hyenas (*Crocuta crocuta*). Using a randomization test, we analysed baboon presence patterns within three 24-hour time blocks before and after the occurrence of a predator. There was no significant decrease in baboon presence following a predator event, suggesting the absence of reactive temporal avoidance in baboons. These results suggest that baboons may rely on alternative predator-avoidance strategies, such as early detection, sentinel behavior, or aggressive retaliation. This study highlights the importance of sample size in detecting behavioral responses and highlights the possible limitations of camera traps in capturing arboreal escape strategies.



**Keywords:** predator-prey interactions, *Papio spp*., randomization test, anti-predator behavior, camera trap

## 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). In response, prey species have evolved a diverse range of behavioural 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).

Behavioral adaptations can be classified into proactive and reactive responses (Broekhuis et al., 2013; Courbin et al., 2016; Creel, 2018; Palmer et al., 2021; Say-Sallaz et al., 2023). Proactive responses are behavioral strategies prey adopt before encountering a predator to reduce predation risk by anticipating threats rather than reacting after a predator appears (Creel et al., 2008; Broekhuis et al., 2013; Creel et al., 2014). These adjustments operate over broad spatial and temporal scales, such as home ranges or seasonal cycles (Droge et al., 2016). For example, Burchell's zebra (*Equus quagga burchellii*) regularly move away from previous lion (*Panthera leo*) encounter sites, such as water holes, to reduce the risk of predation (Thaker et al., 2011; Courbin et al., 2016; Say-Sallaz et al., 2023). Reactive responses, in contrast, are immediate reactions triggered by the direct 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. These responses include fleeing the

area, alerting surrounding group members, or engaging in aggressive retaliation towards the threat (Cowlishaw, 1994; Lingle & Pellis, 2002; Isbell et al., 2018). For example, white-tailed deer (*Odocoileus virginianus*) flee upon detecting coyotes (*Canis latrans*), whereas mule deer (*Odocoileus hemionus*) may choose to actively retaliate (Lingle & Pellis, 2002).

Non-human primates (NHPs), as a prey species, have evolved different strategies in response to predation pressure. Some species such as the hamadryas baboons (*Papio hamadryas*), anticipate by forming large coalitions across troops at roosting sites to enhance group protection (Schreier & Swedell, 2012). In white-faced capuchins (*Cebus capucinus*), individuals increase vigilance near the ground, as they are more exposed to terrestrial predators (Campos & Fedigan 2014). Regarding reactive responses, many species use alarm-call systems as a response to the occurrence of a predator, such as white-faced capuchin and vervet monkeys (*Chlorocebus pygerythrus*) (Seyfarth et al., 1980; Fichtel et al., 2005). These calls help individuals select an appropriate response, such as fleeing, hiding, attacking the predator, or even attempting to rescue captured group members (Perry et al., 2003; Meno et al., 2013). Baboons (*Papio spp.),* bonobos (*Pan paniscus*) and colobine monkeys (*Colobus guereza*) seek refuge in elevated areas as a reactive response, relying on tree canopies and/or cliffs as escape routes while foraging on the ground, to reduce their vulnerability to terrestrial predators (Cowlishaw, 1994; Von Hippel, 1998; Isbell et al., 2018; Druelle et al., 2020).

Among NHP species, baboons encounter a diverse range of predators due to their broad geographic distribution (Buse, 1980; Cowlishaw, 1994; Jooste et al., 2013; Isbell et al., 2018). In southern, eastern and central Africa, their predators include large carnivores such as lions, leopards (*Panthera pardus*) and spotted

95 hyenas (*Crocuta crocuta*) (Busse, 1980; Jooste et al., 2013; Dröge et al., 2017; Isbell
96 et al., 2018). Although these predators infrequently prey on baboons (Busse, 1980;
97 Jooste et al., 2013; Dröge et al., 2017; Isbell et al., 2018), they nevertheless
98 contribute to baboon mortality (Busse, 1980; Cowlishaw, 1994). Leopard and lion are
99 both ambush predator species, but their hunting strategies differ as lions have been
100 observed hunting baboons during the day, whereas leopards hunt both day and
101 night, often targeting baboons at their roosting sites (Busse, 1980; Isbell et al.,
102 2018). Spotted hyenas are cursorial predators (Trinkel, 2010; Wentworth et al., 2011)
103 and although the evidence suggests that they do kill and consume baboons as prey,
104 they may only target baboons when the opportunity arises as opposed to actively
105 hunting them (Buse 1980; Cowlishaw, 1994; Trinkel, 2010; Wentworth et al., 2011).

106 These different predation strategies necessitate different vigilance and escape
107 responses, leading baboons to employ both proactive and reactive responses to
108 mitigate predation risk. Proactively, baboons increase vigilance when away from
109 roost sites or when isolated from group members, enhancing threat detection in
110 vulnerable situations (Fischer et al., 2001). Males also position themselves at the
111 troop's periphery, acting as a guardian for more vulnerable troop members (Surie et
112 al., 2023). Reactively, baboons demonstrate adaptability through aggressive
113 predator mobbing, where they collectively confront and harass predators to deter
114 attacks (Bailey, 1993; Cowlishaw, 1994; Jooste et al., 2013; Isbell et al., 2018).
115 However, it remains unclear whether baboons actively move away from predator
116 encounter sites as part of their antipredator strategies (Allan et al., 2021).

117 Most studies on baboon-predator interactions have primarily used direct in-
118 field observations (Busse, 1980; Hill et al., 2007; Allan et al., 2021). While these
119 methods provide valuable insights, they can be invasive, costly, and may influence

animal behavior due to the observer's presence (Busse, 1980; Basille et al., 2015; Latombe et al., 2014). Camera traps offer a non-invasive, cost-effective alternative for long-term monitoring across large areas, while minimising human disturbance (Newey et al., 2015).

This study analyses camera trap data from three study sites in South Africa and one in Tanzania, to test whether olive baboons (*Papio anubis*) and chacma baboons (*Papio ursinus*) exhibit reactive temporal avoidance in response to predators. Specifically, we test two hypotheses: baboons' presence decreases following the occurrence of a predator (H1). The intensity of this response varies based on the predator's hunting strategy (H2): we predicted a greater decrease in baboons' presence after the occurrence of an ambush predator (lions and leopards) than after a cursorial predator (spotted hyenas). As semi-arboreal animals, baboons can escape cursorial predators by seeking refuge in elevated areas such as trees or cliffs, however leopards may continue their pursuit into a tree, thereby forcing the baboon troop to move out of the area. (Busse, 1980; Trinkel, 2010; Wentworth et al., 2011; Isbell et al., 2018).

## Materials and methods

*Study site selection and description*

This study utilized data from the ongoing camera trap monitoring project *Snapshot Safari*, which spans multiple countries (Swanson et al., 2015; Pardo et al., 2021). We used data from three sites in South Africa (Pardo et al., 2021) and one site in Tanzania (Swanson et al., 2015, data publicly available at Dryad:

http://dx.doi.org/10.5061/dryad.5pt92). The focus was on two baboon species: chacma baboons, primarily distributed in southern Africa, comprising South Africa, Botswana, Zimbabwe and Namibia (Stone et al., 2013), and olive baboons, which occupy the northern regions of central Africa, ranging from Mali to Ethiopia, Kenya, and north-western Tanzania (Zinner et al., 2011).

Of the 32 sites available from the *Snapshot Safari* project, those included in this study were selected based on data availability. Sites were selected only if all three target predators (lions, leopards, and spotted hyenas) were present along with baboons. After such selection, the southern 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 (APNR, 24°20'S - 31°20'E; Figure 1C). Serengeti National Park (SER, 2°19'S - 34°49'E; Figure 1D), in Tanzania, was the sole study site for olive baboons. All four study sites were located within the savanna biome, characterised by open grasslands interspersed with 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 of the savanna biome (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. Elevations range 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). APNR 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 APNR vegetation is highly variable, with isolated tree canopies and a continuous grass understory (Scholes & Archer, 1997). SER, located in Tanzania, spans 25,000 km² and is part of the East African savanna biome, characterized by vast grasslands interspersed with scattered trees (Swanson, 2015).

*Camera trap data*

The data for MAD, TSW, and APNR were collected between June 2017 and November 2019 (29 months), while data for SER were collected between June 2010 and May 2013 (35 months). 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, whereas camera trap placement in the APNR followed a random allocation layout (sensu Meek et al., 2014), based on habitat and geography (see Pardo et al., 2021 for a more detailed description of the camera-trap network in the South African sites; and Swanson et al., 2015 for the Tanzanian site). A total of 355 camera traps (Cuddeback's Professional Series x-change, white flash in South Africa, and Scoutguard (SG565) incandescent cameras in SER) were deployed across the four study sites.

In MAD, TSW and APNR, each camera trap was directed with the infrared trigger facing towards game paths where animal presence had been confidently identified through the presence of scats and/or spoor. In SER, cameras were directed based on vegetation cover, avoiding areas of high grass density to avoid blank images (i.e. a frame or sequence of frames that do not contain animals). The

192 camera traps were enclosed in steel casings and fixed at a height of 0.5-1 m above
193 the ground (Swanson et al., 2015; Pardo et al., 2021). To minimize glare caused by
194 the rising and setting sun, the camera traps were oriented to face as far North or
195 South as possible. Each camera trap was programmed to take three images for
196 every motion detection during the day and one at night (Pardo et al., 2021; Swanson
197 et al., 2015). The sensitivity of each camera trap was set to a medium level (50-75%)
198 to minimize false triggers caused by windblown vegetation. No lures were used to
199 attract any species to the camera trap sites.

200 Capture events (i.e. any single image or consecutive series of images initiated
201 by an animal-trigger, regardless of the number of individuals present in the image)
202 were classified using two methods: (i) the citizen science program Zooniverse
203 (www.zooniverse.org; Swanson et al., 2015), which utilizes the general public to
204 identify animal species in camera trap images, was used exclusively for data
205 collected from SER; (ii) for the three South African sites, species identification was
206 performed by trained laboratory technicians using TrapTagger
207 (www.wildeyeconservation.org).

208 Five camera traps were removed from the MAD dataset that were positioned
209 specifically near waterholes, as predator-prey interactions may likely differ at
210 waterholes due to the trade-off between the need for scarce resources (i.e. water)
211 and predator avoidance (Edwards et al., 2016). The present study used a total of
212 350 camera traps, distributed as follows: ($n_{MAD}$ = 41; $n_{TSW}$ = 28; $n_{APNR}$ = 56; $n_{SER}$ =
213 225). After removing duplicate capture events, the final number of capture events for
214 each of the species of interest was: chacma baboons (n = 1,694), olive baboons (n =
215 1,556), lions (n = 4,554), leopards (n = 442), and spotted hyenas (n = 7,410).

216 *Statistical analyses*

217 To assess whether baboon occurrences after a predator event were lower
218 than expected by chance, we used a randomisation test to compare the observed
219 presence of baboons after the predator event to the ones obtained under the
220 assumption of non-avoidance behavior (Niedballa et al., 2019; Zhang & Zhao, 2023).
221 We calculated the total number of baboon occurrences following all predator events,
222 for each predator species independently. This was done for three consecutive 24h
223 time blocks after each predator event: 0-24 after the predator event, 24-48 hours
224 after the predator event and 48-72 after the predator event. Extending the
225 observation period beyond 72 hours post predator event was avoided due to the
226 difficulty in associating the prey species occurrence with the original predator capture
227 event (Courbin et al., 2016; Swinkels et al., 2023). We further analyzed baboon
228 occurrences before the predation event to establish a baseline of their presence and
229 assess whether any observed decline was linked to the event. This allows us to
230 determine the strength of the predation effect while accounting for natural
231 fluctuations in baboon activity. The analysis of baboon occurrence before a predator
232 event was also conducted in 24-hour intervals over a 72-hour period.

233 We excluded any predator events that occurred within the 72 hours following
234 the camera's deployment and within 72 hours of the end of the camera's operational
235 lifespan to prevent missing data in any pre- or post-encounter time blocks. In
236 addition, we applied a 30-minute time-to-independence filter exclusively to predator
237 capture events, retaining the central capture event within a cluster of consecutive
238 detections as the main event for a given predator. This threshold aligns with previous
239 studies that showed that increasing the independence interval has minimal impact on
240 observed activity patterns of large carnivores (Meek et al., 2014; Peral et al., 2022).

Retaining the central event instead of the first event as usually done in the literature, ensures symmetry when testing for predator-avoidance before and after the predator event in our study design.

To obtain the distribution of baboon occurrences under the null hypothesis (non-avoidance of predators), we randomised the dates of each predator capture event 1,000 times (while preserving their original timing to maintain natural diel activity patterns) and estimated, for each randomised data set, the total number of baboon occurrences in each time block. We excluded any camera trap observation period with a lifespan of < 30 consecutive days to avoid restricting the randomization process. Predator events captured by cameras with a shorter lifespan can only be randomized within a limited date window, which would produce unreliable results.

For each 24-hour time block, we evaluated whether baboon occurrences deviated significantly from a distribution under the assumption of non-avoidance of predators. To do so, we calculated the *P-value* for each time block as the proportion of iterations in our randomization procedure in which the number of baboons was superior or equal to the observed number of baboons before the predator event, and inferior or equal to the observed number of baboons after the predator event. All data processing and analyses were performed using R software (version 4.4.0; R Core Development Team, 2022).

*Validation of the randomization approach*

To validate the randomization approach, we tested our method on Burchell's zebras in APN. Burchell's zebras are known to display reactive temporal avoidance

behavior 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 0–24-hour time block, after lion capture events.

APN had the highest number of lion capture events among the South African sites ($n_{APN}$ = 197, $n_{MAD}$ = 39, $n_{TSW}$ = 87). Although SER had higher numbers of both lions ($n_{SER}$ = 4,266) and Burchell's zebra ($n_{SER}$ = 70,577), analysing these data revealed too computationally intensive using our randomisation procedure. Additionally, the number of Burchell's zebras ($n_{APN}$ = 2,267) was of the same magnitude as the number of baboons in SER, which represents our largest dataset in terms of baboon capture events ($n_{SER}$ = 1,556), making it a suitable comparison point.

To assess the effect of sample size on the analyses, we performed 50 random subsets of Burchell's zebra capture events in APN to match the number of baboon capture events ($n_{APN}$ = 500; see Table 1). This created a down sampled data set, for which we conducted the randomization analysis for each iteration and calculated the frequency of significant versus non-significant p-values.

# Results

*Method validation: predator-avoidance in Burchell's zebras*

Burchell's zebras showed significant reactive temporal avoidance 0–24 hours after the occurrence of lion in APNR (*P-value* = 0.018, Figure 2), providing support for the soundness of our randomisation approach. However, after taking a subset of

Burchell's zebra capture events to match the number of chacma baboon capture events in APNR, we could no longer detect this response 0-24 hours following a lion occurrence (mean *P-value* = 0.160, supplementary figure 1). Despite this absence of significance, a general trend of avoidance remained observable in this species (Figure 2).

*Predator-avoidance in baboons*

Obtained results did not show any significant temporal avoidance in baboons in response to the occurrence of our selected cursorial predator, spotted hyena, across any time block (0–24, 24–48, or 48–72 hours) in any of the three study sites in South Africa (all *P-values* > 0.05, Figure 3, supplementary table 1). Similarly, there was no evidence of baboons displaying reactive temporal avoidance following the occurrence of any of the two ambush predators tested here, namely lions and leopards (all *P-values* > 0.05, Figure 3, supplementary table 1). However, in APNR, baboon presence increased significantly 48–24 hours before the occurrence of lion (*P-value* = 0.001) and 24–0 hours before the occurrence of spotted hyena (*P-value* = 0.003, Figure 3).

In SER, where the number of baboon capture events exceeded those at all South African sites (SER 3.11 times higher than APNR, 4.01 times higher than MAD and 2.11 times higher than TSW, Table 1), and was close to the number of Burchell's zebra capture events in APNR, we still did not detect significant reactive temporal avoidance of baboons in response to any predators tested (all *P-values* > 0.05, Figure 3, supplementary Table 1). Consistent with observations in APNR, baboon occurrences in SER were significantly higher than expected under the assumption of non-avoidance of the predator 24–0 hours before the occurrence of

lion (*P-value* = 0.043, Figure 3). Additionally, baboon occurrences in SER increased significantly 24-0 hours before the occurrence of leopard (*P-value* = 0.019) but showed no significant increase before spotted hyena occurrences (Figure 3).

# Discussion

Our results suggest that chacma and olive baboons do not exhibit any significant reactive temporal avoidance toward any predator (ambush or cursorial) in any of the four study sites (Figure 3), thus invalidating both baboons' presence decreases following the occurrence of a predator H1 and the intensity of this response varies based on the predator's hunting strategy H2. In contrast, Burchell's zebra showed reactive temporal avoidance toward lions within the 0–24-hour time block following the occurrence of lion (Figure 2), as expected given previous observations (Thaker et al., 2011; Courbin et al., 2016; Say-Sallaz et al., 2023). After reducing zebra capture events (to match the highest number of baboon capture events), this significant decrease was no longer observable, suggesting that sample size may impact our ability to detect avoidance response. Although we cannot rule out the problem of statistical power for baboons, the non-significant results in SER (in which the number of baboon occurrences are close to that of zebras in our validation test) suggest the absence of reactive avoidance behavior in olive baboons, and probably chacma baboons.

The absence of reactive temporal avoidance in baboons may be explained by their reliance on alternative predator avoidance strategies. Lima and Dill (1990) proposed that the probability of prey survival increases with the prey's ability to successfully detect and effectively avoid or interrupt the threat as early as possible. By doing so, prey might be able to prevent the predation attempt and reduce their

335 energetic costs of being displaced from a favorable area. Baboons are highly social
336 primates that exhibit sentinel behavior, where one individual monitors for threats
337 while the rest of the troop forages (Horrocks et al., 1986; Bezerra et al., 2008) and
338 use contact barks to signal the presence of a predator (Bailey, 1993; Cowlishaw,
339 1994b; Jooste et al., 2013; Isbell et al., 2018). This altruistic threat detection
340 mechanism may reduce energy expenditure among kin and be favoured over the
341 forced displacement of the entire troop as described in meerkats (*Suricata suricatta*)
342 (Santema & Clutton-Brock, 2013; Rauber et al., 2018).

343 Additionally, moving away from the area at risk does not necessarily imply
344 horizontal displacement for arboreal species. Baboon troops are known for using
345 refuge areas, such as trees or cliffs, employing a vertical escape strategy
346 (Cowlishaw 1997a; Fischer et al. 2001; Isbell et al. 2018). This strategy protects
347 them from terrestrial predators such as spotted hyenas and lions, which are less
348 adapted to climbing (Buse 1980; Cowlishaw 1994). Refuge-based avoidance
349 behaviors have been documented in other species worldwide, including the Nubian
350 ibex (*Capra nubiana*), mule deer (*Odocoileus hemionus*) and klipspringer
351 (*Oreotragus oreotragus*) (Hayward et al. 2006; Hochman & Kotler 2007; Druce et al.
352 2009; Iribarren & Kotler 2012). Similarly to these species that focus their foraging
353 efforts on areas closer to cliffs, rocky outcrops, or higher ground, baboons might
354 favor foraging in areas with sufficient tall trees as an escape route, a mechanism
355 difficult to capture with the camera-trap setup used in this study.

356 When interaction with a predator is inevitable, baboons have been described
357 to respond with aggressive retaliation (Buse, 1980; Hayward et al., 2006; Bailey,
358 1993; Cowlishaw, 1994; Jooste et al., 2013; Isbell et al., 2018). A review by
359 Cowlishaw (1994) analysed predation success rates on baboons across 14 sites in

360 multiple countries. This study showed that leopards were twice as successful as
361 lions and spotted hyenas when preying on baboons. However, when baboons
362 retaliated, they successfully deterred predation in 93% of cases, and in four of 11
363 observed predation attempts, baboons killed the attacking leopard. This behavior is
364 predominantly exhibited by male baboons in both chacma (Cowlishaw, 1994; Isbell
365 et al., 2018) and olive (MacCormick et al., 2012) baboons, owing to their larger teeth
366 and body size (Virgadamo et al., 1972; Galbany et al., 2015; Johnson, 2003). Such a
367 response could decrease predation attempts rate by lowering the predator's chance
368 of successful capture and their interest in the species (Lima & Dill, 1990; Cowlishaw,
369 1994; Alberts, 2018; Isbell et al., 2018). In response to these effective anticipatory
370 anti-predator strategies, predators may simply not actively hunt baboons and focus
371 their efforts on more cost-effective prey such as ungulates. Therefore, the predators
372 would then be viewed as less of a threat by baboons which would consequently be
373 less inclined to leave the area after the arrival of a predator.

374 Despite these results, we cannot completely rule out the possibility that we
375 lacked sufficient statistical power to detect reactive temporal avoidance in our South
376 African sites. To capture the true prey and predator densities, more cameras may be
377 necessary, as is shown by Si et al. (2014) and Evans et al. (2019) with coyotes,
378 whereby increasing the number of cameras by one at each capture site, the
379 probability of detecting the species was four times higher. In addition, it has been
380 shown that the ability to detect spatio-temporal avoidance with camera trap data
381 depends on both interaction strength and sample size (Niedballa et al. 2019). This
382 suggests that detection remains constrained by species-specific activity patterns and
383 the number of observations, reinforcing the need for specific survey design.
384 Optimizing camera density and placement seems essential to mitigate biased

detection, particularly for species with low detection probabilities or complex habitat use.

## Conclusion

This study contributes to broadening our understanding of predator-prey dynamics in two non-human primates' species. The potential absence of reactive temporal avoidance in chacma and olive baboons raises important questions about the variability of their anti-predator strategies, not only in savannah biomes but also across other environments in response to different predators (Zinner et al., 2011; Stone et al., 2013). Interspecific interactions are complex, and species have a wide array of behavioral responses at their disposal to avoid interactions, such as partitioning space or resources instead of time (Morales-Castilla et al., 2015). This study highlights the potential influence of sample size on the detectability of behavioral responses when using camera traps, as illustrated by the loss of significance of reactive temporal avoidance in Burchell's zebra after reduction of the sample size. Limitations in camera trap detection range (i.e. camera traps density and vertical detection capabilities) further emphasize the challenges of accurately quantifying prey-predator interactions among arboreal and low-density species. Future research should prioritize increasing sample sizes and optimizing camera trap configurations to enhance detection probabilities.

## Authors' contributions

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

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## 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 Labelled 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

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 capture events for the species of interest in Associated Private Nature Reserves (APNR), Madikwe Game Reserve (MAD), Tswalu Kalahari Private Wildlife Reserve (TSW) (South Africa, 2017-2019), and Serengeti National Park (SER, Tanzania, 2011-2013). A 30-minute independence interval was applied on the predator detections (see Material and methods section for more details).

| Species | Scientific name | No. of capture events in MAD | No. of capture events in TSW | No. of capture events in APNR | No. of capture events in SER |
|---|---|---|---|---|---|
| Lion | *Panthera leo* | 39 | 87 | 197 | 4,266 |
| Leopard | *Panthera pardus* | 43 | 8 | 168 | 228 |
| Spotted hyena | *Crocuta crocuta* | 187 | 11 | 1,676 | 5,303 |
| Chacma baboon | *Papio ursinus* | 388 | 806 | 500 | 0 |
| Olive baboon | *Papio anubis* | 0 | 0 | 0 | 1,556 |
| Burchell's zebra | *Equus quagga* | 5,099 | 828 | 2,267 | 70,577 |

720 **Supplementary table 1.**
721
722 P-values calculated by comparing the observed occurrences of chacma baboons
723 (*Papio ursinus*) and olive baboons (*Papio anubis*) after a predator event (lion,
724 leopard, spotted hyena) to the distribution of occurrences produced by randomizing
725 the predator event under the assumption of non-avoidance, across six-time blocks
726 (see material and methods section for more details).

| Site | Prey species | Predator species | (-72 to -48 hr) | (-48 to -24 hr) | (-24 to 0 hr) | (0 to 24 hr) | (24 to 48 hr) | (48 to 72 hr) |
|---|---|---|---|---|---|---|---|---|
| MAD | Chacma baboon | Lion | 0,158 | 1 | 1 | 0,894 | 0,46 | 0,459 |
| | | Leopard | 1 | 0,105 | 1 | 0,807 | 0,813 | 0,509 |
| | | Spotted hyena | 0,899 | 1 | 0,91 | 0,753 | 0,235 | 0,085 |
| TSW | Chacma baboon | Lion | 0,451 | 0,32 | 0,042 (***) | 0,924 | 0.686 | 0,348 |
| | | Leopard | 1 | 1 | 0,118 | 0,804 | 0,661 | 0,791 |
| | | Spotted hyena | 1 | 1 | 1 | 0,94 | 0,765 | 0,724 |
| APNR | Chacma baboon | Lion | 0,645 | 0,001 (***) | 1 | 0,503 | 0,241 | 0,415 |
| | | Leopard | 0,555 | 0,714 | 0,536 | 0,563 | 0,123 | 0,606 |
| | | Spotted hyena | 0,921 | 0,064 | 0,003 (***) | 0,202 | 0,47 | 0,152 |
| SER | Olive Baboon | Lion | 0,935 | 0,219 | 0,043 (***) | 0,589 | 0,507 | 0,87 |
| | | Leopard | 0,714 | 0,613 | 0,019 (***) | 0,386 | 0,071 | 0,636 |
| | | Spotted hyena | 0.637 | 0.378 | 0.257 | 0.997 | 0.266 | 0.847 |

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## Figure legends

**Figure 1. Map of the four study sites in South Africa and Tanzania.** A) Madikwe Private Game Reserve (MAD; n = 41 camera traps); B) Tswalu Kalahari Game Reserve (TSW; n = 28 camera traps) and C) Associated Private Nature Reserves (APNR; n = 56 camera traps) in South Africa. D) Serengeti National Park (SER; n = 225 camera traps) in Tanzania. The green boundaries represent the borders of the study areas, the red circles represent the camera trap locations, with their assigned code printed above. *P. ursinus* occurs in all three South African sites, and *P. anubis* occurs only in Serengeti National Park, Tanzania.

**Figure 1. Map of the four study sites in South Africa and Tanzania.** A) Madikwe Private Game Reserve (MAD; n = 41 camera traps); B) The Serengeti National Park (SER; n = 225 camera traps) in Tanzania; C) Tswalu Kalahari Game Reserve (TSW; n = 28 camera traps) and D) Associated Private Nature Reserves (APNR; n = 56 camera traps) in South Africa. The green boundaries represent the borders of the study areas, the red circles represent the camera trap locations, with their assigned code printed above. Pictograms are included to show the presence of *P. ursinus* (indicated for all three South African sites) and *P. anubis* (indicated only for the Serengeti National Park in Tanzania).

**Figure 2. Distribution of Burchell's zebra occurrences obtained from the randomized dataset (n = 1,000) in APNR (Associated Private Nature Reserves) before and after a lion event.** Each panel corresponds to one of six consecutive 24-hour time blocks relative to the predator's occurrence: [-72 to -48 hours before], [-48 to -24 hours before], [-24 to 0 hours before], [0–24 hours after], [24–48 hours after], and [48–72 hours after]. The black vertical lines represent the observed

number of zebra occurrences for each time period. “*” illustrates significant *P-values* (calculated as the proportion of randomized datasets in which zebra occurrences were equal to or lower than the observed value).

**Figure 3. Distribution of baboon occurrences obtained from the randomized dataset (n = 1,000) across different sites and predator category combinations, with each panel representing a distinct time period before and after the predator event.** Each panel corresponds to one of the six consecutive 24-hour time blocks relative to the predator’s event: [-72 to -48 hours before], [-48 to -24 hours before], [-24 to 0 hours before], [0–24 hours after], [24–48 hours after], and [48–72 hours after]. The red vertical lines represent the observed number of baboon occurrences for each site-predator-time period combination. “*” illustrates significant *P-values* (calculated as the proportion of randomized datasets in which baboon occurrences were equal to or lower than the observed value). Colors indicate the predator species: blue for spotted hyena; green for leopard; and red for lion. Sites abbreviations: TSW: Tswalu Kalahari Private Wildlife Reserve; SER: Serengeti National Park; MAD: Madikwe Game Reserve; APNR: Associated Private Nature Reserves.

**Supplementary Figure legend.**

**Supplementary Figure 1. Distribution of *P-values* from the randomization test assessing the effect of lions on zebra occurrence in APNR (Associated Private Nature Reserves) within the 0–24 hours following a lion event.** The test was conducted on randomly down sampled zebra occurrence datasets (n = 50). The red dashed line indicates the *P-value* threshold of 0.05, marking the significance level for detecting deviations from random expectations.

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**Figure 1**

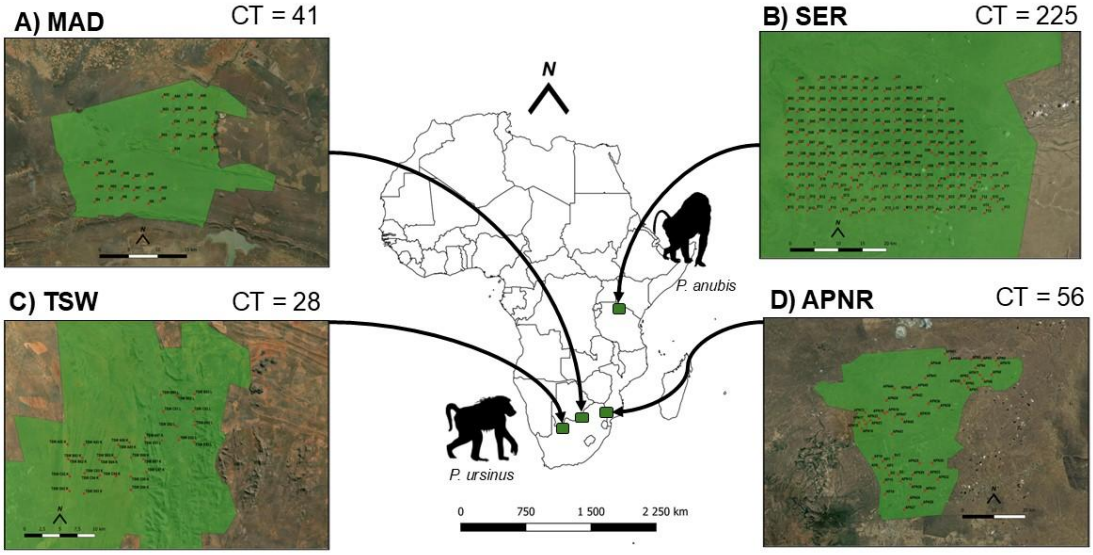
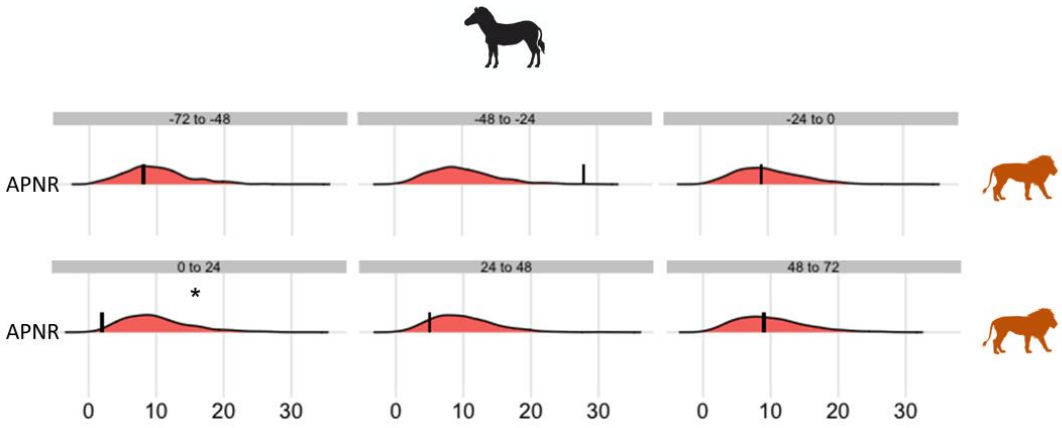
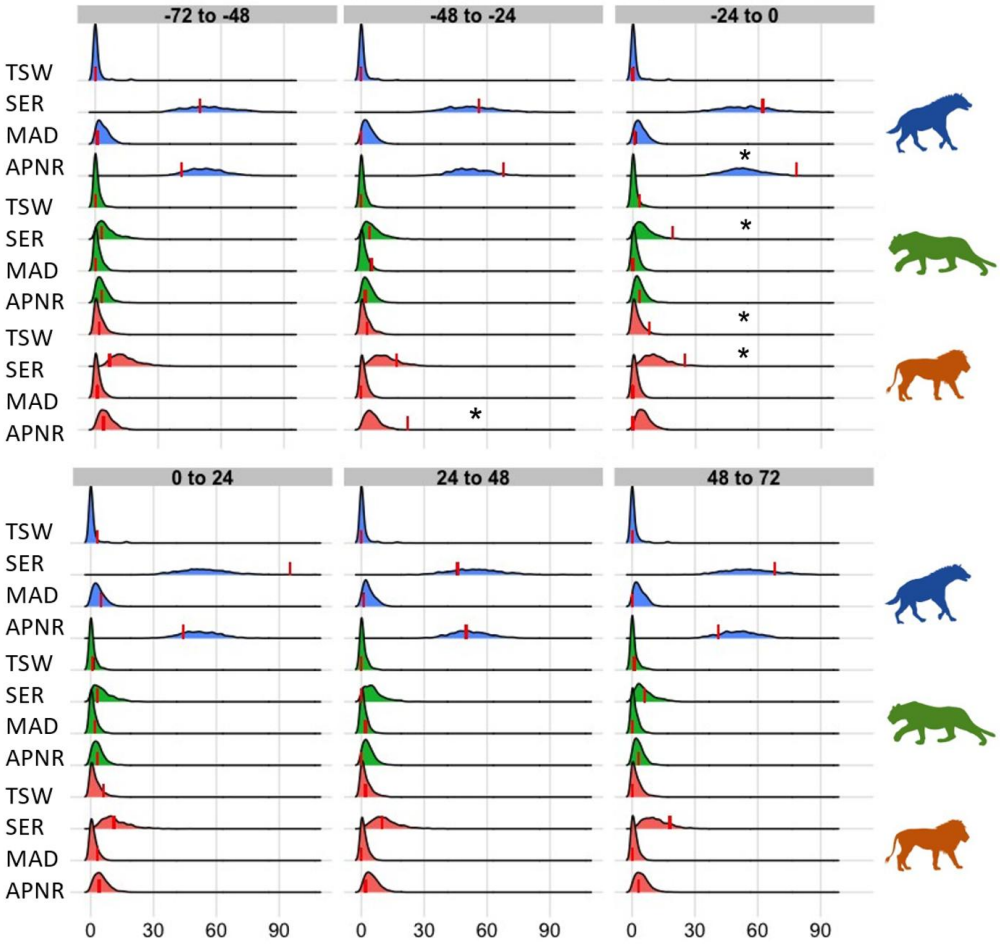



**Figure 2**



786 **Figure 3**

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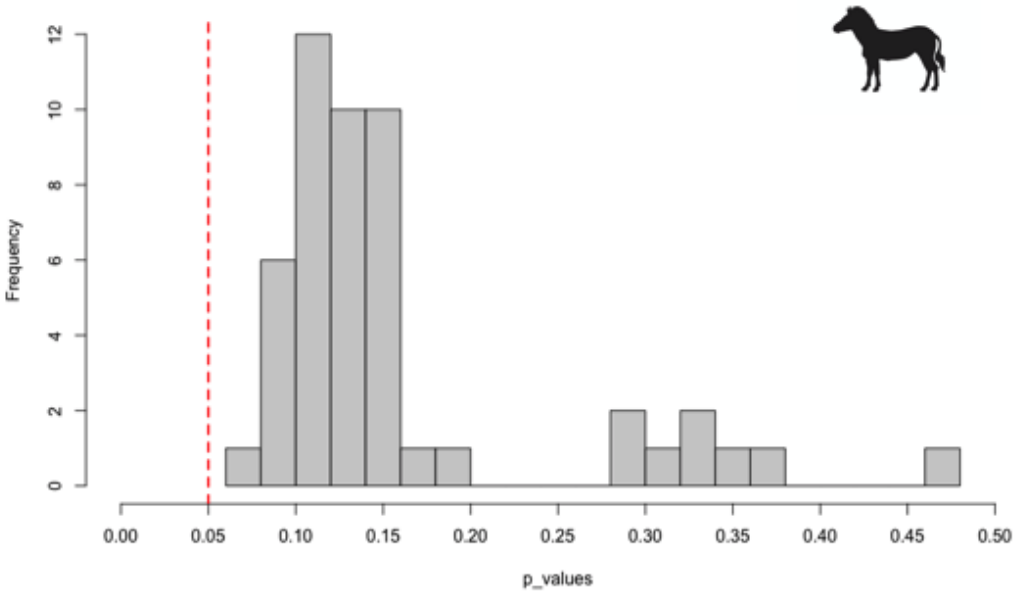
790 **Supplementary Figure 1.**

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