

# The impacts of reintroducing cheetahs on the vigilance behaviour of two naïve prey species

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**Rewilding is a conservation strategy used to restore ecosystems to previous states and can involve the reintroduction of large carnivores into areas from where they had been previously extirpated. Whilst rewilding has been important for ecosystem functioning, it can have negative implications for naïve prey that have had no exposure to the presence of large carnivores. Therefore, understanding prey responses to the reintroduction of predators is crucial for management and conservation. We assessed the effects of reintroduced cheetahs (*Acinonyx jubatus*) on the vigilance of two species of naïve prey: the steenbok (*Raphicerus campestris*) and the springbok (*Antidorcas marsupialis*). We hypothesized that both species would increase their vigilance behaviour post-cheetah reintroduction, but that the steenbok would demonstrate a greater response due to their smaller body size and more solitary nature. To test this, we compared the vigilance of both species before and after the reintroduction of cheetahs. Both species increased vigilance within one year post-cheetah reintroduction, but the steenbok demonstrated a much stronger response with a ~70% increase in the percentage of time spent vigilant post-cheetah reintroduction. Springbok levels of vigilance were lower (~50% increase), which we suggest is a function of body-size and/or grouping behaviour. Importantly, we show that naïve prey species are able to exhibit a rapid response to the reintroduction of large carnivores. However, the variation in responses highlights the importance of species-level monitoring after large carnivore reintroductions.**

**Keywords:** cheetah, prey body-size, prey grouping behaviour, steenbok, springbok, vigilance.

## INTRODUCTION

Over the past few centuries, humans have accelerated species loss and the degradation of ecosystems through overexploitation and habitat change (Pereira & Navarro, 2015). In more recent years, socio-economic changes and shifts in public attitudes have resulted in attempts to offset these large-scale effects (Boitani & Linnell, 2015). Rewilding is among the many conservation strate-

gies undertaken to restore ecosystems to their previous 'wild' states, and is based around the reintroduction of large predators and the services they provide to ecosystems (Soulé & Noss, 1998). Large carnivores can have important functions, including regulating populations of prey, which can have subsequent cascading effects to lower trophic levels (Terborgh & Estes, 2010; Ripple *et al.*, 2014). Beyond top-down effects, rewilding is also important for the conservation of carnivore species (Wolf & Ripple, 2018).

Rewilding has been particularly successful in ecosystems in Europe, North America, and parts of Africa, where top predators have been reintroduced into areas from where they had

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been previously extirpated (Hayward & Somers, 2009). For example, gray wolves (*Canis lupus*) were reintroduced to Yellowstone National Park in North America in 1995 after a 70-year absence (Ripple & Beschta, 2003). Following the reintroduction, wolf numbers increased, leading to a decrease in elk (*Cervus elaphus*) numbers (Ripple & Beschta, 2012). In Europe, the Eurasian lynx (*Lynx lynx*) was first reintroduced between 1970 and 1974 into the Bavarian Forest National Park in Germany, with subsequent reintroductions between 1982 and 1987 into the Bohemian Forest in the Czech Republic (Heurich *et al.*, 2012). Following reintroductions, roe deer (*Capreolus capreolus*) survival decreased due to predation by lynx (Heurich *et al.*, 2012; Andr n & Liberg, 2015). Whilst the reintroduction of predators requires careful consideration of predator spatial and resource requirements, additional consideration is necessary for species that may be preyed upon by these reintroduced predators. Thus, understanding the response of prey to the reintroduction of apex predators is crucial for the management and conservation of all species involved.

Predators exert both lethal and non-lethal effects on prey species (Lima, 1998), which can alter prey behaviour, distributions across the landscape, as well as population and community dynamics (Laundr  *et al.*, 2001; Preisser *et al.*, 2005; Creel *et al.*, 2007; Chamaill -Jammes *et al.*, 2019). Whilst lethal effects of predators on prey are represented by the direct killing of prey, the non-lethal effects predators exert on prey can have the greatest impact on prey through behaviourally-mediated indirect effects on resource acquisition, space use and management (Creel & Christianson, 2007; Chamaill -Jammes *et al.*, 2019). It is the subsequent behavioural responses of prey species to the non-lethal effects of predation that can have substantial ecological significance because these responses can elicit cascading effects within ecosystems (Valeix *et al.*, 2009; Breviglieri, *et al.*, 2017; Chamaill -Jammes *et al.*, 2019).

For gregarious prey species, including many species of ungulates, some of the most common behavioural responses to perceived risk are increasing individual vigilance as well as increasing group size to capitalize on both dilution (*i.e.* reducing the probability of risk) and detection (*i.e.* the 'many eyes' effect; Creel *et al.*, 2014; Schmitt *et al.*, 2014; Schmitt *et al.*, 2016; Stears *et al.*, 2020). However, these responses carry

costs that can have potential implications for fitness, including decreased time available for foraging and mating (Brown & Kotler, 2004; Creel *et al.*, 2014), increased competition with other herd members (Beauchamp, 2009), and increased stress (Clinchy *et al.*, 2004, 2013) that can ultimately influence growth, reproduction, and survival (Lima & Dill, 1990). For highly gregarious herbivore species, variation in herd size can off-set individual vigilance (Underwood, 1982), whereas in solitary or pair-forming species, individual vigilance is not influenced by variation in herd size, but rather only by perceived risk associated with features of their predators and their habitats (*e.g.* Lagory, 1986). Given the costs associated with increasing vigilance, elevated vigilance levels are typically associated with immediate perceived risks (Lima, 1998; Brown & Kotler, 2004; P riquet *et al.*, 2010, 2012). For example, greater kudu (*Tragelaphus strepsiceros*) demonstrate higher levels of vigilance in the presence of lions (*Panthera leo*), but dedicate more time to resource acquisition in their absence (P riquet *et al.*, 2010). By contrast, in areas with minimal predation risk, high investment into anti-predator behaviours is unnecessary and costly, and individuals are expected to invest less time in anti-predator behaviours and spend more time pursuing other activities (*i.e.* foraging) to increase fitness (Lima & Dill, 1990; Creel *et al.*, 2007).

Another factor that influences prey investment in vigilance behaviour is prey body size, which can influence both the physiological needs of the prey species as well as the level of risk that the prey might experience due to differences in predator-prey preferences (Underwood, 1982). With respect to differences in predation pressure, in diverse predator-prey systems, larger-bodied prey species typically have fewer predators than smaller-bodied prey species (Le Roux *et al.*, 2019). Moreover, differences in body size within a prey species can also translate to differences in predation risk because some predators select certain prey demographic classes over others (Clements *et al.*, 2014; Makin & Kerley, 2016). These variations in risk across prey of differing body sizes can lead to dissimilarities in the behaviours that prey employ to reduce their perceived risk. For example, in a study of a diverse ungulate community, Underwood (1982) found that the amount of time devoted to vigilance declined with increasing body size. This decline in vigilance with increasing body size could be a result of lowered

perceived risk associated with either larger-bodied herbivores having fewer predators than smaller-bodied herbivores, or because larger-bodied herbivores have a better view of their surroundings, thus requiring them to make fewer or shorter scans for potential threats (Underwood, 1982). Regardless of whether the scan quality or number of predators is driving the observed relationship between herbivore body size and vigilance, differences in body size across prey species shape their anti-predator behaviours based on their perceived risk of predation.

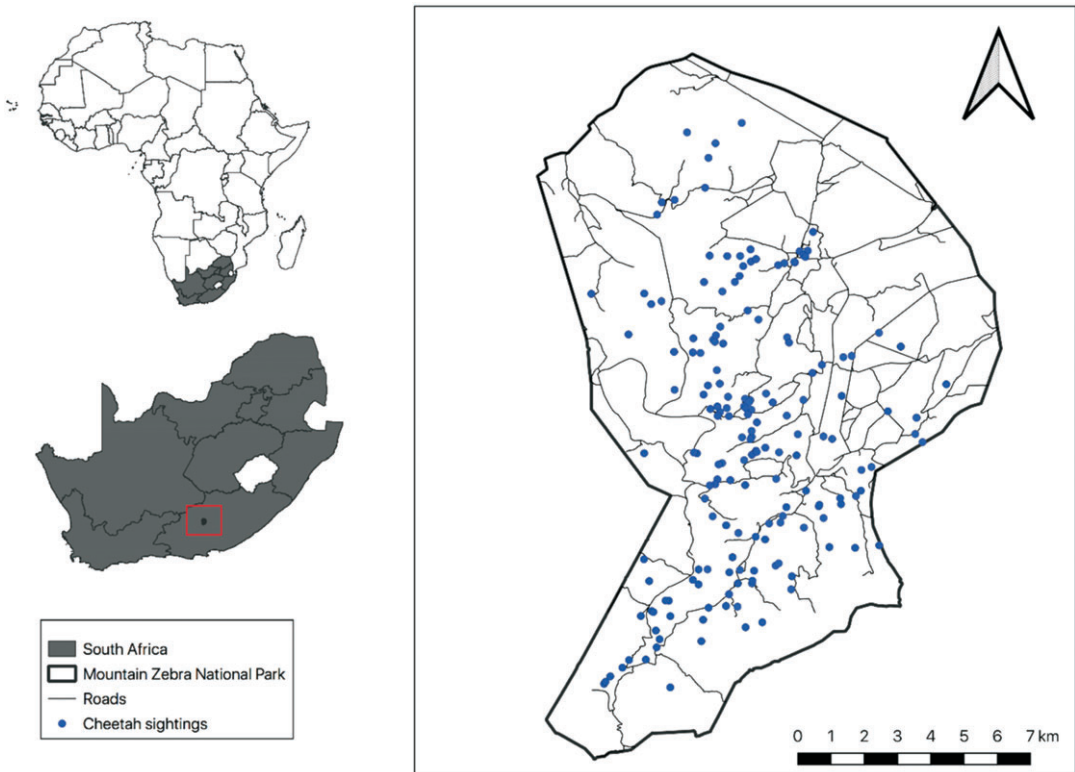
In South Africa, apex predators are being reintroduced to restore ecosystems to previous states and for tourism purposes (Miller *et al.*, 1999; Hayward *et al.*, 2007), and are therefore widespread. Here, we used a model South African system, where before the reintroduction of cheetahs (*Acinonyx jubatus*), ungulate species were exposed to no large predators. We aimed to assess the effects of a cheetah reintroduction on the vigilance behaviour of two potential prey species of differing body sizes and grouping

behaviour: the predominantly solitary ~11 kg steenbok (*Raphicerus campestris*) and the gregarious ~40 kg springbok (*Antidorcas marsupialis*). Both species fall within the preferred prey weight range for cheetahs (Hayward *et al.*, 2006; Mills & Mills, 2017), and thus the reintroduction of cheetahs should elicit a vigilance response in both prey species. While we predicted that both species would increase their vigilance behaviour (both total time spent vigilant as well as number of scans) after cheetah release, we also predicted that the solitary, smaller-bodied steenbok will show a proportionally greater response than springbok due to their smaller body size and more solitary nature.

## METHODS

### Study site

Our study was conducted in Mountain Zebra National Park in the Eastern Cape province of South Africa (hereafter MZNP, 32°18'S, 25° 24'E; Fig. 1). The National Park is approximately 284 km<sup>2</sup>,



**Fig. 1.** Cheetah sightings in the Mountain Zebra National Park situated in the Eastern Cape Province, South Africa (obtained from VHF collar data).

characterized by an arid climate with a mean rainfall of 400 mm (Mucina & Rutherford, 2006), with vegetation ranging from open grasslands to densely vegetated drainage lines. Apex predators were extirpated from MZNP around the end of the nineteenth century, but many ungulate species persisted (Skead *et al.*, 2007; Parker, 2021). Smaller mesopredators such as black-backed jackals (*Canis mesomelas*) also likely persisted (Parker, 2021). Thus, until the reintroduction of four cheetahs (two adult females and a coalition of two adult males) to MZNP in May 2007, there were no large predators present for over 100 years.

### Vigilance data

To determine if and how the two prey species altered their vigilance behaviour in response to the cheetah reintroduction, we collected vigilance data from steenbok and springbok, before and after the reintroduction of the cheetahs. Thus, any changes in the vigilance behaviour of steenbok and springbok would likely be due to the reintroduction of cheetahs. We collected our pre-release data from May 2006 to April 2007 and post-release data from June 2007 to October 2008. Data were collected opportunistically.

Focal individuals of both steenbok and springbok were located while driving on the park road network from 2 hours after sunrise to 2 hours before sunset. We made vigilance observations using binoculars from a stationary vehicle parked on the road (*i.e.* we never went off-road to gather data). To minimize observer-directed vigilance, observations were conducted from about 50 m away so as to not disturb the behaviour of focal individuals. Moreover, prior to starting an observation, we ensured that focal animals displayed no vigilance towards us. We observed each focal individual for 5 min (*e.g.* Matson *et al.*, 2005; Périquet *et al.*, 2010) or until the focal animal went out of sight during observations with a minimal threshold set at one minute. We did not sample from solitary springbok to best represent their behaviours while in herd-settings, nor from situations where there were other species within 100 m of our target species to control for possible mixed-species effects (see Schmitt *et al.*, 2014; Schmitt *et al.*, 2016; Stears *et al.*, 2020), neither did we sample from females with offspring present to eliminate maternal effects (Laundré *et al.*, 2001). We initiated an observation when an individual had its head down feeding. An individual was considered vigilant from the moment it lifted its

head above shoulder level and scanned the surrounding environment (Hunter & Skinner, 1998; Mooring *et al.*, 2004; Matson *et al.*, 2005; Cameron & Du Toit, 2005). During an observation, we noted the total time an individual was vigilant as well as the number of vigilance events the individual made (the number of times an individual lifted its head per minute). For each focal individual, we recorded the total number of individuals in the group, the proximity to cover (near or far, *i.e.* <10 or >10 m), as well as the location of where the observation occurred within the park. Given that steenbok are either solitary or sometimes found in pairs, we typically sampled a single individual of the pair. For springbok, we typically sampled a single individual from the centre of the herd (similar to Bednekoff & Ritter, 1994); however, on several occasions we sampled multiple individuals (maximum of three). On average (mean  $\pm$  S.E.), springbok herds consisted of  $9 \pm 0.85$  individuals, though sampled herds ranged in size from 2–40 individuals. We accounted for these variations in herd size statistically by including herd size as a covariate in our models (see below). Moreover, to avoid pseudo-replication within a herd, we calculated mean individual vigilance per herd as per Schmitt *et al.* (2014, 2016) and Stears *et al.* (2020). To account for any differences in observation time, we transformed all vigilance observations to a percentage of time spent vigilant and mean number of vigilance events per minute. We sampled both species before and after cheetahs were reintroduced into MZNP (steenbok pre-release:  $n = 26$  individuals, 24 herds (steenbok herds were always pairs of animals); steenbok post-release:  $n = 23$  individuals, 18 herds; springbok pre-release:  $n = 47$  individuals, 42 herds; springbok post-release:  $n = 52$  individuals, 37 herds). Due to the terrain of MZNP, once cheetahs were released, they did not use the entire reserve (Fig. 1). Thus, we limited vigilance observations of our two focal species post-release to areas where cheetah were regularly found based on collar data (Fig. 1).

### Statistical analyses

We used two separate models for each species to determine how the reintroduction of cheetahs altered 1) the mean percentage of time that a herd/individual was vigilant, and 2) the mean number of vigilance events per minute. To determine how the mean percentage of time that a herd was vigilant varied before and after cheetah release, we used a Generalized Linear Model with

a Binomial Distribution and a logit-link function. For both models, we included 'pre- vs post-cheetah release' as the main factor. To determine the mean number of vigilance events per minute, we used a Generalized Linear Model with a Tweedie distribution and log-link function. We used a Tweedie distribution because our scan data set contained a range of zero and positive values (Jørgensen, 1987). Model assumptions were verified following the protocol described in Zuur *et al.*, (2010). To control for variation in herd size, we used total number of individuals in a herd as a covariate (see Schmitt *et al.*, 2014, 2016, Stears *et al.*, 2020). Initially, we also included distance to cover as a main factor for all models; however, upon finding that this was non-significant, we later removed it from the model. Data were back-transformed for graphical representation.

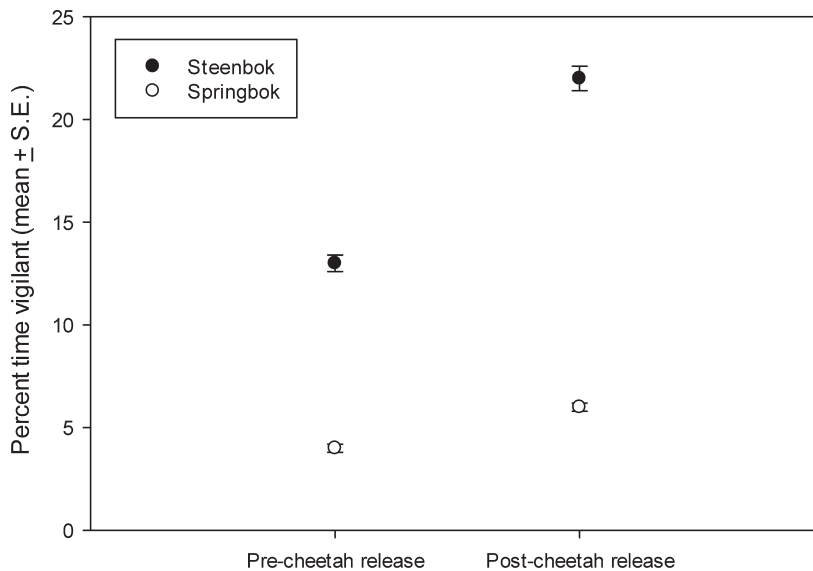
## RESULTS

We found that both steenbok and springbok increased the percentage of time they spent vigilant after cheetahs were reintroduced into MZNP (steenbok:  $\chi^2 = 187.030$ ,  $P < 0.001$ , springbok:  $\chi^2 = 61.466$ ,  $P < 0.001$ , Fig. 2). The covariate of herd size in the percent time spent vigilant model was non-significant for springbok ( $\chi^2 = 2.666$ ,  $P = 0.103$ ), but was significant for steenbok ( $\chi^2 = 6.913$ ,  $P = 0.009$ ). Steenbok increased the percentage of time they devoted to vigilance from

(mean  $\pm$  S.E.)  $13 \pm 0.004\%$  to  $22 \pm 0.006\%$  in response to cheetahs being reintroduced, while springbok increased their percentage vigilance by  $\sim 2\%$  (from  $4 \pm 0.002\%$  to  $6 \pm 0.002\%$ ). However, when we examined whether either species altered the number of vigilance events that they conducted per minute before and after cheetah reintroduction, we found that there was no significant difference between the two time frames (steenbok:  $\chi^2 = 0.558$ ,  $P = 0.455$ , springbok:  $\chi^2 = 4.072$ ,  $P = 0.08$ ). Thus, instead of conducting more vigilance events per minute, both steenbok and springbok increased the lengths of their scans. For both species, the covariate of herd size was non-significant (springbok:  $\chi^2 = 0.139$ ,  $P = 0.709$ ; steenbok:  $\chi^2 = 0.015$ ,  $P = 0.903$ ).

## DISCUSSION

Our study illustrates the behavioural adjustments exhibited by two prey species in response to a reintroduced apex predator. Specifically, we found that both species increased the percentage of time they devoted to vigilance after cheetahs were reintroduced into MZNP. However, we found that steenbok showed a much greater anti-predator response than springbok, in which steenbok increased the percentage they devoted to vigilance from  $\sim 13\%$  to  $\sim 22\%$  of time, which represents  $\sim 70\%$  increase, while springbok increased their percentage vigilance by  $\sim 2\%$  (from  $4\%$  to  $\sim 6\%$ ), which represents a  $50\%$  increase. It is worth



**Fig. 2.** Mean percentage of time ( $\pm$ S.E.) that steenbok and springbok devoted to vigilance before and after cheetah were reintroduced. Black dots represent steenbok and open dots represent springbok.

highlighting that because of increased time spent vigilant in the presence of predators, steenbok will likely have less time, in absolute terms, on a daily basis to carry out other activities such as foraging, etc., which may not be sustainable.

The vigilance levels for both prey species were low prior to the cheetah reintroduction compared to typical vigilance values found in the literature for many other herbivore species exposed to higher predation risk (*i.e.* large carnivores present; Underwood, 1982; Makin *et al.*, 2017, 2018; Stears *et al.*, 2020). For example, impala (*Aepyceros melampus*), when herding with conspecifics in high predation risk areas (*i.e.* areas that contain key predators: lions and cheetahs), devote up to ~22% of their time to vigilance while foraging (Hunter & Skinner, 1998). However, impala that live in areas with a lower risk of predation (*i.e.* lions and cheetahs are absent, but smaller carnivores such as black-backed jackals are present), devote only ~8–9% of their time to vigilance when feeding (Hunter & Skinner, 1998). Thus, our findings of ~4% and ~13% of time invested to vigilance by steenbok and springbok, respectively, prior to the cheetah reintroduction, while still low, is within the range of that for other species under low levels of predation risk (*i.e.* larger carnivores absent, but smaller carnivores present).

Whilst we observed an increase in the percent time devoted to vigilance behaviour of springbok after the cheetah reintroduction, springbok vigilance levels remained relatively low (~6% time devoted to vigilance). However, these levels of vigilance are consistent with other studies in predator-rich areas that have demonstrated springbok dedicate ~6% (Burger *et al.*, 2000) and ~8% (Bednekoff & Ritter, 1994) of their time to vigilance. Similarly, the vigilance responses of steenbok after cheetah reintroduction were also consistent with Underwood (1982) who found that steenbok devoted  $15 \pm 5\%$  S.E. of their time towards vigilance in high predation risk areas, which is within range of our observation of  $22 \pm 2.3\%$  S.E. Thus, the vigilance responses we observed for both springbok and steenbok post-cheetah release are reflective of those elicited by these species that are not naïve to predation (*i.e.* have long-term prior experience with the predator).

In addition to having differences in the absolute scale of percent time spent vigilant after predator reintroduction (*i.e.* steenbok: 22% vs springbok 6%), we also observed differences in the magni-

tude of their responses. Steenbok exhibited a much greater response in their vigilance efforts compared to springbok (~70% vs ~50% increase, respectively). Given that we controlled for herd size in our statistical analyses to account for any variation in vigilance associated with a range of herd sizes, it is unlikely that our observed differences are purely a result of herding behaviour. Moreover, other gregarious prey species such as zebra (*Equus quagga*), sable (*Hippotragus niger*), and greater kudu demonstrate relatively large increases in the percentage time devoted to vigilance when faced with elevated predation risk (Makin *et al.*, 2018; Stears *et al.*, 2020). Whilst springbok grouping behaviour likely contributed to the differences between the two species in vigilance behaviour, it is unlikely to be solely driving their smaller increase in percentage of time devoted to vigilance while feeding. The differences between the magnitude of response from steenbok and springbok could have also been due to several other mechanisms: 1) aspects related to prey body size including differences in predator preference and quality of scans across the environment resulting from better abilities to see, or 2) differences in predator detection methods (*i.e.* reliance on visual vigilance vs hearing or smelling predators).

With respect to body-size, larger-bodied prey species have greater horizontal vision and increased sightlines over vegetation when compared to smaller species (Andersson, 1981; Underwood, 1982). Thus, larger species require fewer or shorter scans to acquire accurate information of the environment, whereas smaller species must revise information on their surroundings more regularly (Andersson, 1981; Underwood, 1982). Similar to our findings, other studies also report a relationship between body mass and vigilance and have shown that larger species exhibit lower levels of vigilance when compared to smaller species (Underwood, 1982; Berger & Cunningham, 1988; Périquet *et al.*, 2012; Creel *et al.*, 2019). Thus, Creel *et al.* (2019) suggests that prey body size is a strong predictor for the restricted effects of predation. Furthermore, smaller-bodied prey can be more susceptible to opportunistic predation from a wider variety of predators (Sinclair *et al.*, 2003; Le Roux *et al.*, 2019). In MZNP, steenbok fall within the preferred prey weight range for cheetahs (Hayward *et al.*, 2006; Mills & Mills, 2017), but may also be more susceptible to opportunistic predation by black-backed jackals, caracals (*Caracal caracal*) and

larger birds of prey, *e.g.* martial eagles (*Polemaetus bellicosus*), which could potentially drive their higher overall levels of vigilance.

With respect to differences in predator detection methods, prey species can use a variety of sensory modes to detect predators. In our study, we focused on visual vigilance; however, this is not the only means prey species use to detect predators. For example, auditory and olfactory cues have been shown to be important in predator detection (Kuijper *et al.*, 2014; Creel *et al.*, 2019; Makin *et al.*, 2019; Valenta *et al.*, 2021). Many prey species have been shown to exhibit strong behavioural responses to conspecific and hetero-specific alarm calls, as well as in response to predator sounds (Palmer & Gross, 2018; Makin *et al.*, 2019). Likewise, herbivores have been shown both to avoid entering as well as limit time spent in areas with predator olfactory cues, such as predator scat (Wikenros *et al.*, 2015; Valenta *et al.*, 2021). Thus, the relatively low levels of visual vigilance observed for springbok may indicate that this species may be more reliant on other predator detection methods.

Our results align with other studies that have shown naïve prey demonstrate vigilance responses post-predator reintroductions even without prior experience of these species (Berger *et al.*, 2001; Laundré *et al.*, 2001; Makin *et al.*, 2018). In our study, a response was observed for both ungulate species in the first year post-cheetah reintroduction. Similarly, following the reintroduction of wolves into Yellowstone National Park, female elk showed an increase in vigilance the first year after reintroduction (Laundré *et al.*, 2001). In addition, Makin *et al.*, (2018) found that several species of African ungulates responded to a predator reintroduction by increasing their vigilance behaviour while foraging in certain habitats within two months of release.

It is worth noting that post-cheetah reintroduction observations began soon after cheetahs had been released so changes in vigilance may have been limited initially. We would expect an initial abrupt increase in vigilance levels during a period of heightened stress, but that this would reduce to similar levels exhibited by prey coexisting with large carnivores throughout their lives. Unfortunately, our data were not sufficient to test for a longitudinal pattern and we suggest that future studies investigate how vigilance changes with time post-large carnivore introduction.

Our findings reveal how quickly naïve prey can

adapt to reintroduced predators, and that responses can vary between species and these differences may be based on variations in grouping behaviour, body-size and/or the method of predator detection. Importantly, when predators are reintroduced into small fenced reserves, such as MZNP, they can have dramatic consequences, including rapid reductions in prey numbers (*e.g.* Tambling & du Toit, 2005; Lehmann *et al.*, 2008), presumably due to prey naïvety and minimal learning which can occur when both adults and young are preyed upon (Berger *et al.*, 2001). Thus, reintroductions of apex predators need to proceed with careful consideration of predator type, the number of predators being reintroduced, the size of area being reintroduced into and type of prey present (Hayward *et al.*, 2007). Globally, large carnivores continue to be reintroduced into areas from which they were previously extirpated, and therefore the findings from our study are pertinent. We demonstrate that prey species are able to learn rapidly, despite no prior experience of large predators (or that species retain basal anti-predator behaviour even in the absence of large predators) but that responses vary at the species level. Our findings are also important with respect to the possible prevention of species extinctions through rewilding; however, we suggest that monitoring individual prey species is critical for such a conservation intervention to be successful.

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#### CONFLICTS OF INTEREST

The authors declare that they have no conflict of interest.

#### ETHICS APPROVAL

All applicable institutional and/or national guidelines for the care and use of animals were followed. As the work was observational, Rhodes University indicated there was no need to provide ethical clearance.

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