Evaluation of lion *Panthera leo* scat as a wild dog *Lycaon pictus* deterrent on game farms

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Short summary

Retaliatory killing of wild dogs in response to game depredation is a major threat to the survival of the free-roaming population. This study aimed to assess the deterrence effect of lion scat on wild dogs and showed that wild dog movements can be modified. Here, we demonstrate a valuable tool for wildlife managers to effectively minimize conflict between farmers and wild dogs. Photograph by Ronja D. Haring.

Abstract

Context. The conservation of the Endangered African wild dog *Lycaon pictus* poses a major challenge to conservationists, because outside the boundaries of protected areas, wild dogs are prone to conflict with farmers. Mitigation measures applicable to game farmers are scarce, leaving them with limited options to reduce wild dog impact. As a result, targeted persecution is a common occurrence. However, wild dogs are subject to intraguild competition with dominant competitors, often resulting in their suppression and spatial displacement. Therefore, olfactory cues of lion presence may trigger an adverse reaction in wild dogs and is a means to manage wild dog movements across the landscape to prevent conflict with farmers.

Aim. The present study evaluated whether wild dogs can be deterred by simulating lion presence.

Methods. By using translocated scent cues in the form of lion scat deployed along the perimeter of plots, lion presence was simulated on game farms where lions were absent. The rate and duration of incursions by wild dogs, collared with GPS trackers, into control and treatment plots were evaluated.

Key results. Wild dog incursion rate dropped by 55.5% while duration of incursion events dropped by 72.7% after treatment was implemented. Unexpectedly, control and treatment plots were equally affected with no significant effect of group on wild dog activity. The magnitude of the treatment effect differed between packs.

Conclusion. The steep drop of wild dog activity after implementation of treatment suggests a deterrence effect. The insignificant effect of group on wild dog activity may be attributed to a spill-over effect of treatment on control plots and a change in the wild dogs' risk perception across the landscape following treatment. The fact that the magnitude of the treatment effect differed between packs indicates that the response to predator cues is likely to be context-dependent.

Implications. The findings present a novel approach to managing free-roaming wild dogs by utilising biologically relevant cues, that may benefit wild dog conservation. There is a need for further research to develop the neglected field of scent studies to provide wildlife-friendly solutions and progress towards evidence-based large carnivore management practices.

Key-words: antipredator behaviour, human–carnivore conflict, interspecific olfactory communication, landscape of fear, non-lethal mitigation measures, odour deterrent, perceived risk, conservation ecology

Introduction

South Africa is home to the ‘Endangered’ African wild dog *Lycaon pictus*, where a free-roaming population comprising 20% of the country’s animals occurs outside of protected areas (mean 79 ± 18 adults and yearlings) (Nicholson et al. 2020). This free-roaming population is an important stronghold for the species but is prone to anthropogenic mortality on private land. An estimated 39% of free-roaming animals are killed through direct persecution that results from human-wild dog conflict (Davies-Mostert et al. 2016). As anthropogenic mortality is additive to natural mortality, it can undermine the viability of the free-roaming population (Woodroffe et al. 2007). For populations of rare carnivores where conservation relies on the protection of individuals and groups as an intact unit, losses can be especially devastating with impacts on the stability and persistence of social units, reproduction, genetic diversity and overall mortality (Haber 1996). In addition, the viability of source populations is compromised if ecological traps outside of protected areas drain the source population of individuals (van der Meer et al. 2013). Consequently, hostility from landowners has led to drastic population declines in the past (Woodroffe and Ginsberg 1999) and, if ongoing, can have substantial impacts on species persistence (van der Meer et al. 2013).

While mitigation measures that address the impacts of large carnivores on livestock farmers are well explored, the potential to mitigate the impact of large carnivores on game farms has received less attention (Shivik 2006). With the rise of the game ranching industry, game is increasingly being used for economic gain and when consumptive wildlife utilisation dominates land use, game farmers tend to express negative attitudes towards wild dogs

(Lindsey et al. 2005). Unlike livestock, game animals cannot easily be herded, rendering most mitigation measures recommended in the literature ineffective for game farmers (Thorn et al. 2015). This limits the farmer's options to reduce wild dog impact, leading to more killing of carnivores (Fink et al. 2020).

Experimental studies under real world conditions that provide evidence of the effectiveness of non-lethal mitigation measures are scarce (Eklund et al. 2017), and manipulations of behaviour have rarely been applied to the conservation of free-roaming wildlife (Linklater 2004). The lack of scientific evidence that supports wildlife-friendly solutions impedes progress towards evidence-based large carnivore management practices (Eklund et al. 2017) and undermines farmers' trust in non-lethal mitigation measures (Young et al. 2018).

The subordinate wild dog is subject to intraguild interactions, involving exploitative and interference competition with dominant competitors such as lions *Panthera leo* (Creel and Creel 1998; Hayward and Kerley 2008). In the Kruger National Park, lions account for 39% of pup and at least 36% of adult deaths (van Heerden et al. 1995), making them the single most important cause of natural mortality (Woodroffe and Ginsberg 1999). Consequently, wild dogs actively avoid lions (Webster et al. 2012) and are displaced from areas where lions are abundant (Swanson et al. 2014). Even when no wild dogs have been killed, packs actively avoid areas with suspected or known presence of lions by making use of indirect cues to asses risk (Webster et al. 2012). Previous research on cheetahs *Acinonyx jubatus* and other mesopredators has revealed that subordinate carnivores are able to avoid direct interactions with dominant competitors by using scent cues (Cornhill and Kerley 2020; Haswell et al. 2018). Olfaction is an exceptionally important and well developed sense in wild dogs (Green et al. 2012). This suggests that olfactory cues might also be used by wild dogs to assess predation risk. Odour sources that indirectly advertise lion presence might act as biologically relevant cues to wild dogs and could be used to create a landscape of fear by altering the wild dogs' perception of risk across space. Therefore, lion scat might hold great potential to function as a conservation tool by modifying wild dog movements across the landscape.

We investigated the effect of lion scat placed along the perimeter of plots defined by linear features on wild dog movements by evaluating wild dog activity within plots, i.e. rate and duration of incursions. We hypothesized that wild dogs are strongly averse to olfactory cues of lion presence, resulting in a reduced rate and duration of incursions after lion scat deployment.

Materials and Methods

Study population and area

The study was conducted on private farms and reserves within the Limpopo Province of South Africa (Fig. 1. Overview of the location of the two study sites, the Mapesu Private Game Reserve and the Lowveld, in the Limpopo Province of South Africa). Collared wild dog packs with an established home range in an accessible area outside of protected reserves were considered for this study. One pack, consisting of seven (±2) adult dogs, ranged freely in the Lowveld Bushveld between Acornhoek and Hoedspruit of the Mopani district. Another pack of two adult dogs occurred within the boundaries of the Mapesu Private Game Reserve (MPGR) in the Mopane Bushveld of the Vhembe district.

At both study sites, rainfall is strongly seasonal, with pronounced rainfall in the summer months between October and April (Rutherford et al. 2006; Venter et al. 2003). On average, annual rainfall varies between 500 and 700 mm in the Lowveld Bushveld (MacFadyen et al. 2018) and 300 to 400 mm in the Mopane Bushveld (Rutherford et al. 2006), with mean temperatures being generally warm all year round (Rutherford et al. 2006; Venter et al. 2003). The uplands of the Lowveld Bushveld are dominated by tall shrublands with *Terminalia* and *Combretum* species, whereas the bottomlands consist of dense thickets to open savannas with *Senegalia nigrescens*, *Dichrostachys cinerea* and *Grewia bicolor* being prominent. The

Mopane Bushveld is mainly characterized by open woodland to moderately closed shrubland dominated by *Colophospermum mopane* (Rutherford *et al.* 2006).

Wild dog packs are exposed to a rich faunal assemblage at both sites, including common antelopes, megaherbivores and large predators (e.g. cheetah, leopard *Panthera pardus* and spotted hyena *Crocuta crocuta*). However, no lions occur on the MPGR nor on any other property included in this study. The MPGR is enclosed by well-maintained 'predator-proof' perimeter fencing, which mostly contains the large mammals.

Pre-experimental stage

Spatial data on wild dog movements were gathered to define the area that was occupied by wild dogs. The data were derived from dogs collared with GPS trackers. One individual per pack had a GPS collar, and the movement of that individual was taken to represent the movement of the entire pack. Wild dogs are highly cohesive and move as a unit (Creel and Creel 1995). No wild dogs were specifically collared for the purpose of this study; instead, wild dogs had already been collared by the Endangered Wildlife Trust (EWT) and associated organisations (i.e. the Mapesu Private Game Reserve). Collars provided four to six GPS fixes per day at varying intervals, providing an adequate sampling frequency for a mobile species that can cover large distances daily (Pretorius et al. 2019). Two to eight weeks of movement data were used to calculate home ranges (95% isopleth) for each site prior to the experiment, after which the privately-owned land within the home range was subdivided into plots. The plots were created based on linear features such as roads, rivers and fences. The size of the plots varied between 0.4 km^2 and 2.65 km^2, averaging ~1.20 km^2, which is large enough to capture location data points but small enough to be logistically feasible. Sample plots were selected randomly and assigned to either the control or the treatment group. The group allocation of the first plot was at random after which the allocation of all following plots alternated from the first plot. To prevent plots of different groups influencing one another, control and treatment plots did not share a boundary. If the random selection of a plot would have led to a common boundary between control and treatment plots, the plot was skipped without replacement to avoid excessive clustering of plots within groups. In the event that plots assigned as treatment plots could not be used as such due to ethical considerations overruling the study design or issues of access, they persisted as potential control plots. The number of control and treatment plots was equal for all sites. Each site had five treatment and five control plots.

Experimental stage

Collar data were used to determine the number of times wild dogs entered a plot (incursion events) and the amount of time they spent within the plot on each occasion, with the 'duration' being defined as the number of consecutive GPS fixes received during incursion events. This was investigated for both the pre-test phase and the test phase. Between mid-April and the end of September '21, covering the denning season, each plot was monitored for four to ten consecutive weeks during both phases. The monitoring time was determined by external factors (e.g. availability of data and access to plots).

During the test phase, for the treatment plots a natural scent barrier was created by placing lion scat along the inner perimeter of the linear feature lining the plot. The lion scat was collected from wildlife sanctuaries up to twice a week and frozen (-14.5 to -20°C) inside sealed plastic containers to retain freshness until the implementation of the experiment. To create a uniform scent note, the frozen scat was pooled to allow scats of different ages to mix. The samples were defrosted one day before use. Along the perimeter of the treatment plots, 110 g (± 5 g) of lion scat was placed every 100 m. Before placement, samples were soaked in 50 ml of water to reinforce the odour by adding moisture. The scat was replaced two to five times at 10-day intervals. Control plots neither received treatment (scat) nor were their perimeters patrolled by vehicle.

Data preparation and analysis

Quantum GIS (ver. 3.14, QGIS Development Team 2021) and RStudio (ver. 3.5.3, R Core Team 2020) were used to conduct a kernel density estimation to identify the home ranges (95% isopleth) of each pack. To calculate the kernel isopleths, the reference smoothing factor was applied, which had performed reliably in past home range calculations for wild dogs (Mbizah et al. 2014). If the estimated home range included areas that were disconnected by hard boundaries (e.g. rivers), and preliminary data had shown that these areas were not utilized by the wild dogs, the home range was edited accordingly (effective home range).

A generalized linear mixed model with a Poisson distribution and a log link was conducted in RStudio to compare the rate and duration of incursions between *groups* (control vs. treatment plots) within each *phase*, before and during the deployment of scat (pre-test and test phase), and between *phases* (pre-test vs. test phase) within each *group* (treatment and control plots). For objective (a) the dependent variable was the count of incursion events, and for objective (b) the count of consecutive GPS fixes during incursion events. To adjust for the variation in the amount of opportunity that existed for each event (differences in the number of GPS fixes per day between collars and in observation days between and within phases), the natural logarithm of 'exposure' (GPS fixes per day multiplied by observation days) was included as an offset variable. Additionally, *pack* was included as a fixed effect and the interactions between *phase* and *pack* as well as between *pack* and *group* were added. Plots were sampled twice, therefore *plot ID* was included as a random factor.

A preselection of variables was conducted to construct a global model. Each explanatory variable was analysed separately to determine its effect on the dependent variable. Except for the main interaction between group and phase, and the variables of particular interest (*group,* *phase* and *pack*), those variables not correlated with the dependent variable ($p > 0.25$) were excluded from further analysis (Bendel and Afifi 1977). The optimal model was then constructed based on the procedure outlined in Zuur et al. (2009) protocol, evaluating the retained parameters in a backward stepwise manner. Statistical significance was assessed at $p < 0.05$.

Contrasts of marginal linear predictions were calculated to allow for the pairwise comparison of group means. The conditional r-squared value for mixed effects models with complex random effects structures was estimated.

Results

The Lowveld pack was sampled twice because it moved to a different area after data collection had been completed at the first site. The effective home range of the Lowveld pack spanned 35.60 km^2 at the first site and 64.04 km^2 at the second site. The Mapesu pack covered 71.76 km^2. In total, 20 plots ($n_{control} = 10$; $n_{treatment} = 10$) were included across sites (Fig. 2).

Rate of incursions

The number of incursions per group per phase averaged 2.30±2.79 ($\bar{x}$±SD) over the study period. The rate of incursion was best explained by a model containing the variables *pack* (p=0.382), *group* (p=0.937) and *phase* (p=0.004) as well as the interactions between *phase* and *pack* (p=0.041) and *phase* and *group* (p=0.972). The conditional r-squared value for the model was 0.609.

Neither pack (Mapesu vs. Lowveld) nor group (treatment vs. control) were associated with the rate of incursions (incidence rate ratio [IRR]±SE: 1.45±0.61, 95% CI [0.63, 3.33], p=0.381; IRR: 1.03±0.42, 95% CI [0.47, 2.28], p= 0.937) and within phases the rate of an incursions did not differ significantly between packs (pre-test phase: IRR: 0.81±0.35, 95% CI [0.36, 1.87], p=0.627; test phase: IRR: 2.58±1.50, 95% CI [0.82, 8.08], p=0.104) or between groups (pre-test phase: IRR: 1.04±0.44, 95% CI [0.45, 2.38], p=0.925; test phase: IRR: 1.02±0.52, 95% CI [0.38, 2.75], p=0.963).

Phase (test vs. pre-test) had a significant effect on incursion rate. During the test phase, the incursion rate was 45% of what it was during the pre-test phase (0.45±0.13, 95% CI [0.26, 0.77], p=0.004). This effect was apparent across packs and groups. In both groups the incursion rate dropped significantly between phases and to a similar extent (Fig. 3). In the control plots, the incursion rate in the test phase was 45% of what it was in the pre-test phase (IRR: 0.45±0.15, 95% CI [0.23, 0.88], p=0.019). Similarly, the incursion rate into the treatment plots in the test phase was 44% of what it was in the pre-test phase (IRR: 0.44±0.17, 95% CI [0.21, 0.94], p=0.033). Both packs reduced their incursion rate during the test phase (Fig. 4), however, dropping by 75%, the incursion rate of the Lowveld pack (IRR: 0.25±0.13, 95% CI [0.09, 0.67], p=0.006) decreased much more than that of the Mapesu pack, where the reduction was 21% and non-significant (IRR: 0.79±0.20, 95% CI [0.48, 1.31], p=0.367).

Duration of incursions

The number of GPS fixes per group per phase averaged 5.5±7.77 ($\bar{x}$±SD) over the study period. The duration of incursion events was best explained by a model containing the variables *pack* (p=0.468), *group* (p=0.225) and *phase* (p<0.0001) as well as the interactions between *phase* and *pack* (p<0.0001) and *phase* and *group* (p=0.268). The conditional r-squared value for the model was 0.881.

Neither pack (Mapesu vs. Lowveld) nor group (treatment vs. control) were associated with the duration of incursion events (IRR: 1.43±0.71, 95% CI [0.54, 3.80], p=0.468; IRR: 1.78±0.85, 95% CI [0.70, 4.453], p=0.225). However, within the test phase, the packs differed significantly from each other. The time the Mapesu pack spent during incursions was 4.52 times more than the time that was spent by the Lowveld pack (IRR: 4.52±2.74, 95% CI [1.38, 14.80], p=0.013). Incursion duration did not differ between groups within phases (pre-test phase: IRR: 1.49±0.71, 95% CI [0.58, 3.79], p=0.258; test phase: IRR: 2.14±1.13, 95% CI [0.76, 6.01], p=0.151). Phase (test vs. pre-test) had a significant effect on incursion duration, which dropped by 73% during the test phase (IRR: 0.27±0.06, 95% CI [0.18, 0.41], p<0.0001). This decrease was apparent across both groups (**Fig. 5**) and packs (Fig. 6). In the control group, the incursion duration in the test phase was 23% of what it was in the pre-test phase (IRR: 0.23±0.06, 95% CI [0.13, 0.39], p<0.0001). Similarly, the incursion duration of the treatment group in the test phase was 33% of what it was in the pre-test phase (IRR: 0.33±0.08, 95% CI [0.20, 0.54], p<0.0001). The Lowveld pack significantly reduced the duration of incursion events to 9% of what it was during the pre-test phase (IRR: 0.09±0.03, 95% CI [0.04, 0.19], p<0.0001), whereas for the Mapesu pack, the reduction was only by 14% and was non-significant (IRR: 0.86±0.15, 95% CI [0.61, 1.21], p=0.392).

Discussion

Our results indicate that wild dog activity was significantly reduced after lion scat deployment. Contrary to our expectations, wild dog activity decreased in both the treatment and the control plots, with no difference detected during the test phase between treatment and control plots. Although both packs reduced their rate and duration of incursions, the decrease in wild dog activity was more pronounced in the Lowveld pack. Consequently, packs behaved significantly different from each other during the test phase when the duration of incursions was investigated.

There are several possible explanations for the apparent lack of differences between treatment and control plots. It is likely that the treatment plots affected the outcome of the control plots. Although plots of contrary treatment did not share a boundary, the distance between plots might have been inadequate. Lions are territorial and the density of scats tends to increase towards the centre of territories due to more intensive use of the core area (Zub et al. 2003). By placing a large amount of scat in a small area, as it was done in this study (~30 to 75 g per 0.01 km^2), the high lion activity found in core areas was mimicked. Since wild dogs avoid areas of high lion activity (Dröge et al. 2017), the treatment could have motivated the wild dogs to increase their distance from such plots as a safety precaution. This assumption is supported by the finding of the Waterberg Wild Dog Initiative that wild dogs moved 5 km or more after being exposed to lion scat compared to less than 1 km prior to each instance of placing the scat (*R Mooney 2021, pers. comm.*). The lack of intergroup differences could also be attributed to the fact that a single farm usually accommodated both control and treatment plots. In the Lowveld, the landscape is severely fragmented and electrified game fences separated the farms at the study site. The permeability of a hard boundary varies among taxonomically related species (Cozzi et al. 2013); whereas wild dogs are notorious for crossing fences with ease, even when electrified (Davies-Mostert et al. 2012), for lions fences represent a nearly impassable obstacle (Cozzi et al. 2013). Apart from the physical capability of an animal to cross a barrier, the barrier's permeability primarily depends on the animal's perception, needs and motivation to cross (Cozzi et al. 2013; Wiens et al. 1985). The inability of lions to cross fences results in creating vacuum-areas that are relatively lion-free and provide spatial refuges for other species. Wild dogs have an explicit perception of risk distribution across the landscape. They will, for example, seek den sites in lion-vacuum areas on private land but return to protected areas daily to hunt (Cozzi et al. 2013). Possibly, the treated farms in this research were perceived as a safe refuge, but once indications of lion presence were detected, the perceived habitat quality was degraded, and the motivation of the wild dogs to cross the fence compromised, leading to reduced wild dog activity on both control and treatment plots.

After treatment had been implemented, the large decrease in wild dog activity during the test phase (56% and 73% for incursion rate and duration, respectively) suggests a deterrence effect of lion scat placement on wild dogs. A decrease in wild dog activity could be a result of seasonal changes unrelated to treatment. In fact, the study period covered the denning season (Mbizah et al. 2014), during which the home ranges of wild dogs may contract by more than two thirds (Pomilla et al. 2015) and habitat selection preferences change as a result of an increased aversion to risk (O'Neill et al. 2020). In addition, wild dogs are a highly mobile species, and a low wild dog activity later in the season might simply reflect that the wild dogs have moved on. However, as it appears from the movement data, the packs did not den that season nor abandon their estimated effective home range. Moreover, based on tracks, it was noted that on multiple (>10) occasions wild dogs diverted from their original path to inspect deposited lion scat nearby (<3 m) before they continued, suggesting that lion scat has relevance to them. Mesopredators are initially attracted towards olfactory cues of apex predators. This behaviour is usually accompanied by increased vigilance and has thus been described as a trade-off between the potential risk of a lethal encounter with the apex predator and obtaining information about a potential food source in the vicinity (Wikenros et al. 2017). Wild dogs, however, rarely scavenge to avoid interactions with dominant competitors (Hayward et al. 2006). Therefore, it is questionable whether the inspection of apex predator scats fulfils the same function in wild dogs as in some of the other mesopredators. Scat conveys information about its producer, and each predator species most likely has its own very unique scent (Apfelbach et al. 2005). Lions are ambush predators (Hopcraft et al. 2005) and territorial (Mosser and Packer 2009), meaning they launch surprise attacks from a close distance and show a high site fidelity. Hence, even aged cues may indicate the actual presence of lions and induce risk assessing and anti-predator behaviour (Bytheway et al. 2013). It should be considered that wild dogs may inspect scat of lions to assess predation risk, ultimately altering their perception of risk across the landscape.

There are several possible explanations why the two packs reacted differently to the lion scat. The response to predator cues is context-dependent. For instance, a shift in habitat as a response to predation pressure is only a viable option if alternative habitat and resources are available (Ward et al. 1997). It has been found that wild dogs avoid lions via spatial partitioning, amongst others, mediated by resource distribution. As a result, territories are larger where lions and wild dogs coexist, not only to allow for the spatial avoidance of lions but also to access resources that became unavailable in the process (Marneweck et al. 2019). In fact, after the experiment the effective homerange of the Lowveld pack had extended by 36%, which indicates spatial partitioning. However, unlike the free-roaming Lowveld pack, the Mapesu pack was confined to a defined area, limiting its potential to adjust their range and explore new resource patches in response to increased predation pressure. If there is no room for escape and the exposure to the risk persists, an animal has to forage in high-risk areas to meet energy demands (Hegab et al. 2015). The lack of avoidance of indirect cues associated with predators presence relates to the fitness costs of avoiding a potential food resource (Ward et al. 1997). Besides, anti-predator behaviours are not limited to spatial responses, but animals have a repertoire of potential responses to predation risk (Hegab et al. 2015). In wild dogs, behavioural plasticity is usually demonstrated on a spatial scale (Dröge et al. 2017) but they will resort to temporal avoidance if necessary (Darnell et al. 2014).

The different responses of packs to cues of lion presence may also be explained by variation in habitat structure between the two sites. When confronted with direct cues of immediate lion presence, wild dogs have been observed to condition their behaviour on ambush risk (Davies et al. 2021; Webster et al. 2012). Where the risk to encounter lions is high, wild dogs shift to sites with a high visibility to allow for the early detection of lions (Davies et al. 2021). Although the likelihood of being ambushed is less where visibility is high, it does not mean that wild dogs fare better in homogeneous open habitats (Webster et al. 2012). In open habitats, wild dogs are more likely to encounter and be detected by dominant competitors, and become prone to interference competition (Creel and Creel 1996). Accordingly, competition refuges such as areas of dense vegetation are advantageous to wild dogs as they are characterized by low lion densities and provide cover (Davies et al. 2021). Hence, in areas of dense vegetation, wild dogs are more likely to display risky behaviours and only avoid the most recent location of lions (Vanak et al. 2013). In essence, wild dog populations can cope with high lion densities by using a mosaic of different habitat structures to evade lions (Davies et al. 2021). Areas with increased visibility are important to defuse situations of immediate risk while dense vegetation provides sheltered habitat. In line with these findings, Webster, McNutt and McComb (2012) suggest that wild dogs' ideal habitat consists of canopied vegetation with a minimal understory (e.g. mature mopane woodlands) and occasional clearings. The canopied vegetation shelters wild dog kills and prevents the dogs from being located by competitors. Simultaneously, the open areas provide resting sites that are safe from ambush attacks (Webster et al. 2012). Although an accurate assessment of landscape heterogeneity and vegetational differences was beyond the scope of this study, the landscape found in the range of the Mapesu pack resembles the description by Webster, McNutt and McComb (2012). It is therefore possible that the Mapesu pack was more likely to show risky behaviour than the Lowveld pack.

Furthermore, responses to predators are modulated by internal factors, such as an animal’s previous experience with predators. In some species, prior experience is necessary before effective antipredator behaviours are exhibited in response to indirect cues of predator presence (Apfelbach et al. 2005). In addition, where predators are present in the natural surroundings of an animal, the fear of predators is continuously reinforced, enhancing the responsiveness to predator cues (Ayon et al. 2017). Experience has been shown to play a vital role in wild dogs.

Predator-naïve wild dogs born in captivity have been shown to underestimate the threat posed by predators, frequently resulting in failed re-introduction efforts (Frantzen et al. 2001). Whereas the range of the free-roaming Lowveld pack includes properties that keep lions, the reserve hosting the Mapesu pack is free of lions. Although the dogs of the Mapesu pack were born and raised elsewhere and likely had exposure to lions prior to capture, by the time plots were treated, the female and the male had at least spent 10 and 24 months in a lion-free environment, respectively. Therefore, the lack of recent exposure to lions may have reduced the pack's sensitivity to indirect cues of lion presence.

Currently, research on the use of scent cues to direct the movement of predators and mitigate conflict is still in its infancy (Apps 2021). This study broadens the current knowledge about the responses of mesopredators to indirect cues of apex predator presence and contributes to a slowly growing body of literature on the use of scent cues to promote human-carnivore coexistence. Notwithstanding the limitations of this study and the need for more research, the findings offer compelling evidence for the potential effectiveness of lion scat as a wild dog deterrent and, where lion scat is available, this inexpensive method of mitigation could be used in attempts to direct wild dogs away from areas where they are prone to persecution. The findings of this study could have positive conservation implications for wild dogs by supporting wildlife managers and encouraging further research in the field of scent studies.

Data availability

The data that support this study were in part obtained from the Endangered Wildlife Trust and Mapesu Private Game Reserve by permission. Hence, data will only be shared upon reasonable request to the corresponding author with permission from the third parties.

Conflicts of interest

The authors declare no conflicts of interest

Declaration of funding

Funding was provided by the Kevin Richardson Foundation. The Foundation was not involved in the preparation of the data or manuscript or the decision to submit for publication.

Authors' contributions

AT, JO, GB and RH conceived the ideas and designed methodology; RH collected the data; PT and RH analysed the data; RH led the writing of the manuscript and AT, PT and JO revised it. All authors contributed critically to the drafts and gave final approval for publication.

Statement on inclusion. Our study brings together authors of different backgrounds, including scientists based in the region where the study was carried out. All authors were engaged early on with the research and study design to ensure that the diverse sets of perspectives they represent was considered from the onset. The research was conducted in close cooperation with the landowners affected by wild dog impact who are important stakeholder in wild dog conservation

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Appendix: Figures

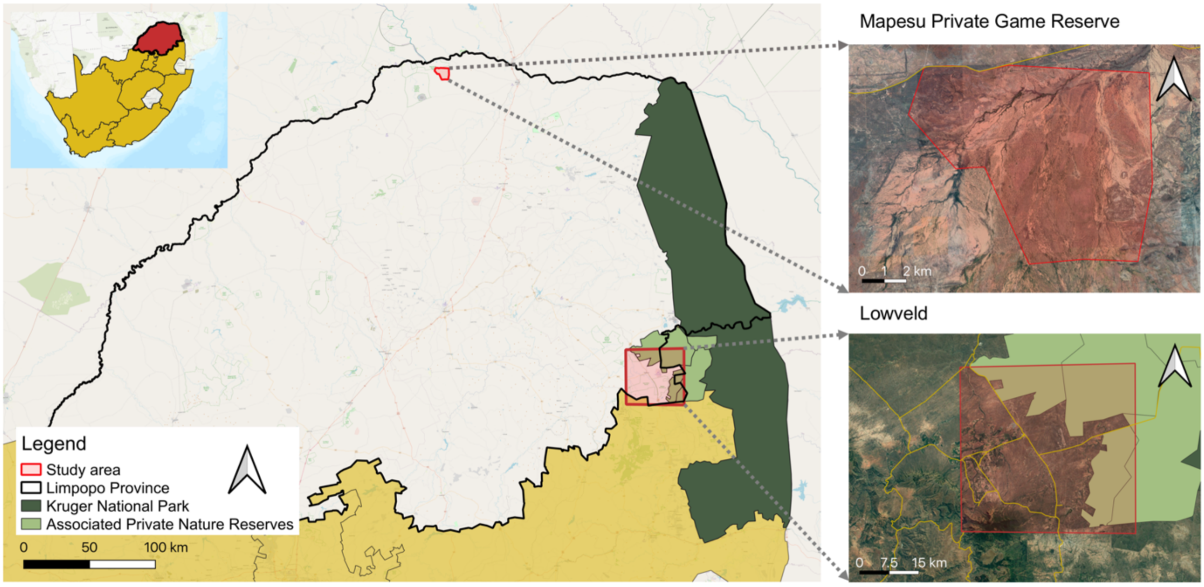

Fig. 1. Overview of the location of the two study sites, the Mapesu Private Game Reserve and the Lowveld, in the Limpopo Province of South Africa.

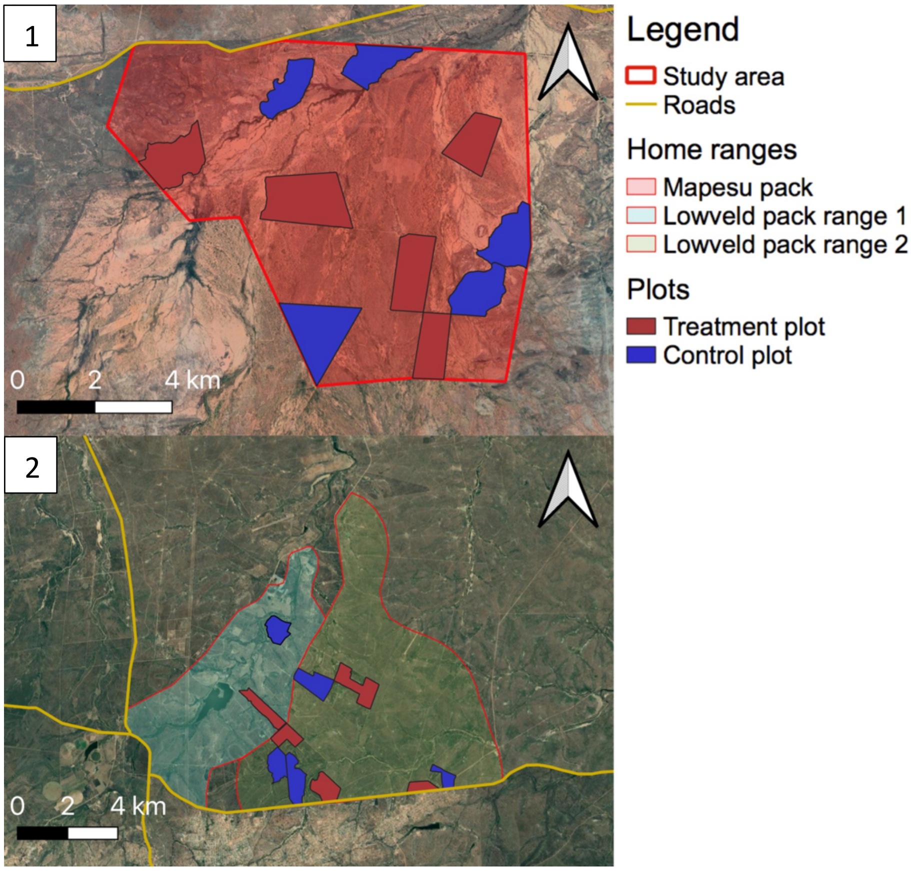

Fig. 2. Display of effective home ranges of 1) the Mapesu pack and the 2) Lowveld pack and the location of treatment and control plots within effective home ranges. Effective home ranges are based on 95% kernel density home range estimations.

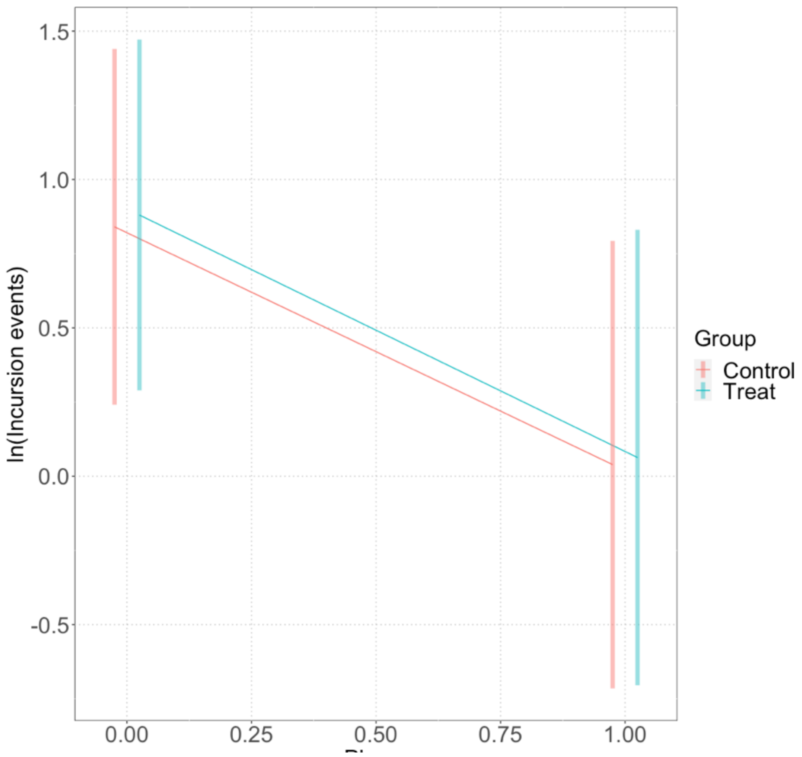

Fig. 3. Estimated number of incursions during the pre-test and test phase for study plots belonging to the control or the treatment group. Error bars represent 95% confidence intervals.

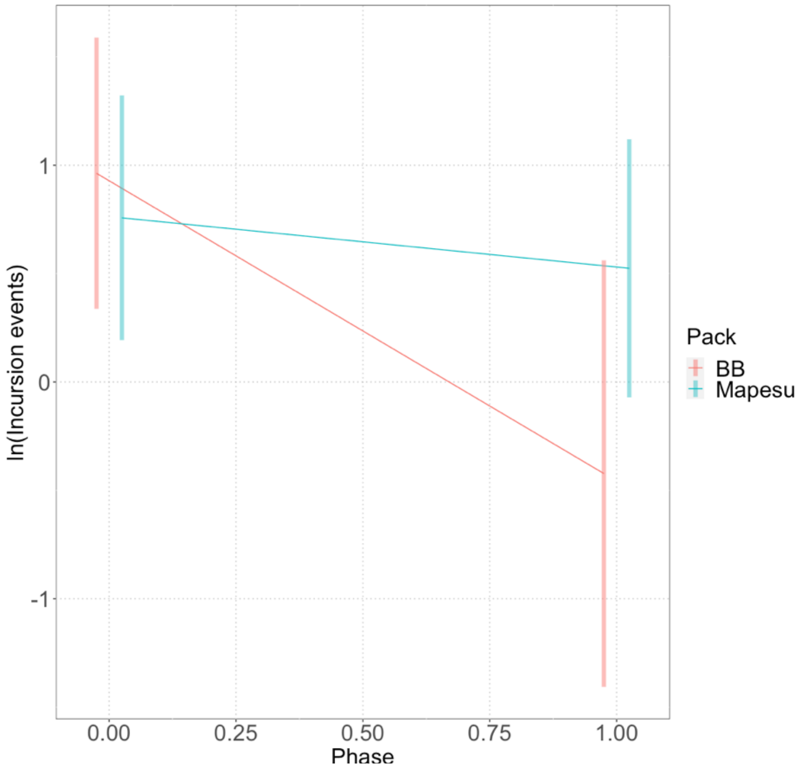

Fig. 4. Estimated number of incursions during the pre-test and test phase for study plots visited by the Mapesu or the Lowveld pack. Error bars represent 95% confidence intervals.

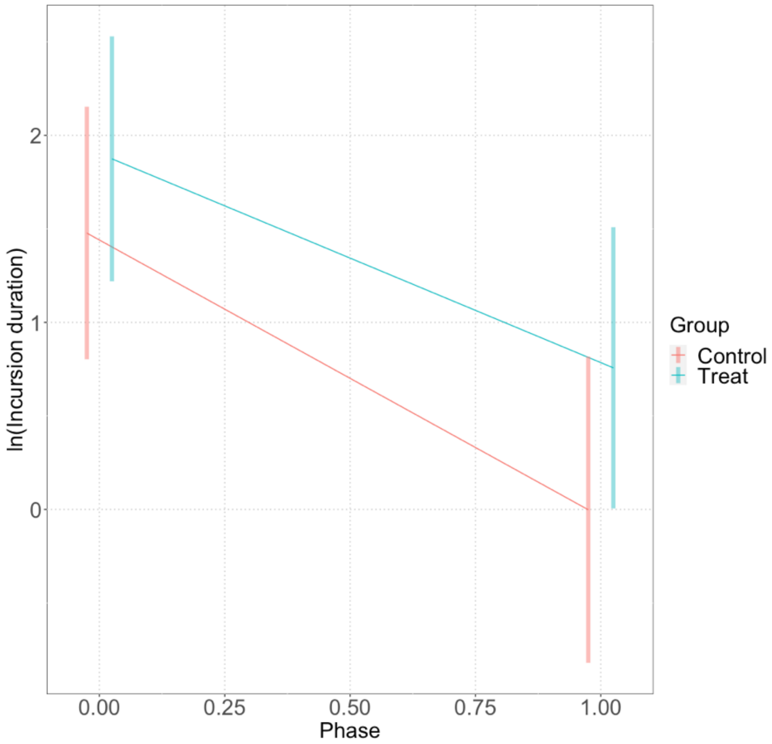

Fig. 5. Estimated duration of incursion events during the pre-test and test phase for study plots belonging to the control or the treatment group. Error bars represent 95% confidence intervals.

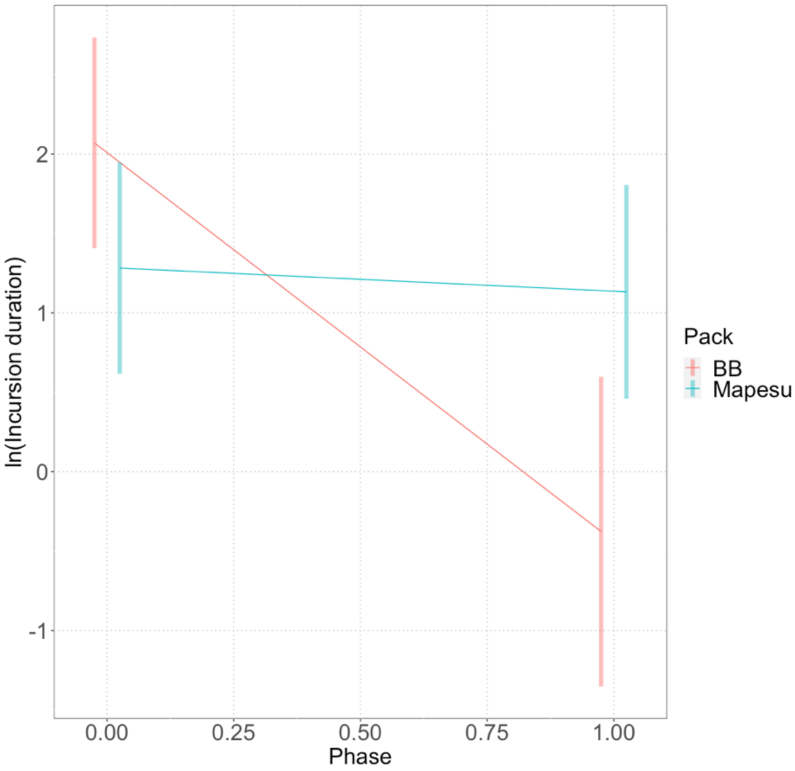

Fig. 6. Estimated duration of incursion events (defined as the number of consecutive GPS fixes received during incursion events) during the pre-test and test phase for study plots visited by the Mapesu or the Lowveld pack. Error bars represent 95% confidence intervals.