Mechanisms facilitating coexistence between leopards (*Panthera pardus*) and their competitors in the Okavango Delta, Botswana

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Abstract

Large carnivores provide key ecological services to ecosystems, and full species assemblages are thought to be important in maintaining full ecosystem function. The African large carnivore guild represents one of the last functionally intact guilds of large carnivores on Earth, but relatively little is known of the mechanisms facilitating coexistence between some of its members. As such, I investigate coexistence mechanisms between leopards (*Panthera pardus*) and their competitors and present four pieces of original research on leopard ecology and monitoring, primarily within the framework of carnivore interactions. To this end, I focus on sympatric populations of wild, but habituated, lions (*Panthera leo*), leopards, African wild dogs (*Lycaon pictus*), and cheetahs (*Acinonyx jubatus*) in northern Botswana. Data were primarily collected through a combination of field-based observations, high-resolution GPS radio collars, and tourist-contributed photographs. I found that at both broad- and fine- scales, leopards were largely resilient to the effects of intraguild competition. Specifically, I found little evidence that spatio-temporal niches were driven by predator avoidance and found limited impacts of competitor encounters on leopard behaviours and movements. In the context of intraspecific competition, my thesis also informs on the optimal scent marking strategies used by leopards to communicate with conspecifics, presumably, in part, to facilitate territory maintenance. Specifically, leopards invested more in maintaining scent marks at home range boundaries and scent marked at higher frequencies on roads. My thesis results also highlight the potential of using tourist photographs to monitor large carnivore densities within protected areas. In sum, my findings provide key insights into the coexistence mechanisms between leopards and their competitors and provide a framework for sustainable citizen-driven wildlife monitoring programs.

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Finally, although I thought of putting this last acknowledgement towards the end of the thesis in order to encourage its recipient to read it, just in case she doesn't make it, many thanks also go to my mother for putting up with me for the past 28 years.

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CHAPTER 1

General Introduction

Carnivores and competition

Through their impacts on a range of factors, including species abundance (Berger and Gese, 2007), distributions (Davis et al., 2018), and behaviours (Balme et al., 2017a), interactions between species can provide key regulating and structuring services for ecosystems (Haswell et al., 2017). Further, the interplay of interactions across multiple linkages of species and their joint effects can lead to synergisms that are important in maintaining full ecosystem function (Ripple et al., 2014). Consequently, the loss of even a single species within an ecosystem can lead to disproportionally large effects relative to that species' density. Unfortunately global biodiversity is rapidly declining (Barnosky et al., 2011), and the drivers of biodiversity loss, which are commonly anthropogenic (Marco et al., 2014), can often lead to the loss of key species and their functions within ecosystems (Prowse et al., 2014).

Large carnivore species, here used to refer to members of the order Carnivora whose average adult body mass exceeds 15 kg (Ripple et al., 2014), are inherently susceptible to the drivers of biodiversity loss because they commonly occur at low densities and have low reproductive rates, reducing their resilience to disturbance and perturbation (Cardillo et al., 2004; Marco et al., 2014). In the case of human persecution, large home ranges can also increase their potential to come into conflict with humans and place protected populations at risk through sink effects (Balme et al., 2010; Woodroffe and Ginsberg, 1998). The loss of large carnivores is, however, concerning as they are often keystone species that play important regulatory and structuring roles within ecosystems (Haswell et al., 2017; Ripple et al., 2014), and they can have disproportionally large effects on the whole biota relative to their low densities (Estes et al., 2011). Large carnivores also often perform key economic services through their provisioning of economic benefits associated with tourism and by acting as flagship species for conservation (Lindsey et al., 2007; Minin et al., 2013). Their loss from ecosystems can lead to trophic cascades that release mesopredators from top-down suppression and that propagate throughout lower trophic levels, in some cases changing the physical environment (Ripple et al., 2014). In Australia, for example, the removal of dingoes (*Canis dingo*) can cause trophic cascades that lead to large scale changes in landscape geomorphology, with possible implications for species at lower trophic levels (Lyons et al., 2018).

Interactions between large carnivores or the interplay of interactions involving multiple carnivore species can shape carnivore impacts on ecosystems (Haswell et al., 2017). For example, the additive effects of sympatric carnivores on prey selection may impact prey densities in much different ways than would have been seen in the presence of any one of the species in isolation (e.g. Ripple and Beschta, 2012). Further, within large carnivore assemblages, the competitive suppression of subdominant species could also have effects that cascade throughout lower trophic levels. Within some landscapes, for example, African wild dogs (*Lycaon pictus*) avoid habitats intensively used by lions (*Panthera leo*) (Creel and Creel, 1996; Groom et al., 2017), and in some areas of Asia, leopard distributions are shaped by avoidance of tigers (*Panthera tigris*), as well as prey availability (Steinmetz et al., 2013). However, wild dogs are thought to suppress prey populations (Ford et al., 2015); as such, their use of habitat patches with low predation risk may lead to reductions in browsing pressures on plant communities within them and be a key component of the overall community structure (Ford et al., 2014). The complex interplay between sympatric large carnivore interactions is thought to play a critical role in structuring ecosystems, and as an extension, intact carnivore assemblages are thought to be a key component in maintaining full ecosystem function (Dalerum et al., 2009; Haswell et al., 2017). The African large predator guild, however, is one of the few remaining functionally intact predator assemblages from the Pleistocene megafauna mass extinction occurring at a local scale (Dalerum et al., 2009). As such, most other carnivore-regulated systems may now reflect a loss of regulatory function relative to pre-extinction systems (Haswell et al., 2017). This makes the African large predator guild a particularly unique study system within which to understand competitor interactions.

The African large predator guild

The African large predator guild (herein referred to as the large predator guild) consists of five large carnivore species: lion, spotted hyaena (*Crocuta crocuta*), leopard (*Panthera pardus*), African wild dog, and cheetah (*Acinonyx jubatus*) that are sympatric across large regions of Africa. Although, it could be argued that brown hyaena (*Parahyaena brunnea*) and striped hyaena (*Hyaena hyaena*) are also members of this guild, I do not include them within this thesis' definition because they are primarily scavengers (Kingdon, 2013; Mills, 2003; Wiesel, 2015) and are often not included within other studies of the large predator guild (e.g. Cozzi, 2012; Hayward and Slotow, 2009; Vanak et al., 2013). Instead, these seven species together are commonly defined as Africa's large carnivore guild (Dalerum, 2009). The African large predator guild, however, will be the study system of this thesis.

A guild is a functional classification of species within the same community that compete for similar resources (Wilson, 1999), and as such, competition within guilds is often fierce. Indeed, species within the large predator guild often have similar prey and habitat preferences, and consequently, the guild exhibits intense interspecific competition (Caro and Stoner, 2003; Hayward and Kerley, 2008). This competition can have implications on the space-use, behaviour, and densities of the guild's competitively inferior members (Balme et al., 2017a; Darnell et al., 2014; Durant, 2000; Groom 2017). Wild dogs are, for example, competitively subordinate to lions and spotted hyaenas, and it is thought that populations suffering high kleptoparasitism due to intraguild competition may be suppressed and, subsequently, susceptible to stochastic events and localised extinctions (Carbone et al., 1997).

Interactions between the guild's two largest (lion and spotted hyaena) and two smallest (wild dog and cheetah) species typically show an asymmetrical dominance hierarchy due to pronounced differences in the mass of individuals/social groups (Creel and Creel, 2002; Groom et al., 2017; Schaller, 1976). However, the outcomes of interactions amongst other guild dyads may often depend on the contexts of encounters (Bailey, 2005; Creel and Creel, 2002). Outcomes of lion and spotted hyaena interactions, for example, largely depend on the ratio and sex of competitors involved (Cooper, 1991; Périquet et al., 2015). Interestingly, leopards have often been ignored in intraguild competition studies, and it remains unclear how intraguild interactions involving the leopard may affect the ecology and behaviour of all species involved.

The African leopard

Leopards are a large solitary felid that, despite being the most widespread large predator in Africa, have now disappeared from an estimated 48–67% of their historical range (Jacobson et al., 2016; Ray et al., 2005). They have the widest habitat tolerance of any wild felid, with the ability to persist in a wide range of habitats, including deserts, rainforests and urban environments (Jacobson et al., 2016; Nowell and Jackson, 1996; Odden et al., 2014). Leopards are an intermediately sized member of the large predator guild, with, on average, an individual body mass greater than wild dogs and cheetahs, but smaller than lions and spotted hyaenas (Table 1). However, their size advantage over wild dogs can quickly shift during encounters, with the individual mass of multiple wild dog pack members combining to provide a competitive advantage (Downer, 2017), and leopards may thus be competitively subordinate to all guild species apart from cheetah.

Although leopard interactions within the Asian large predator guild have been relatively well studied (e.g. Karanth and Sunquist, 2000; Steinmetz et al., 2013), relatively little is known of the interactions between leopards and other large African predator guild species. In this respect, they are arguably one of the least studied guild members. This may be a consequence of pervasive assumptions on the resilience of leopards to interspecific competition because of their catholic prey and habitat selection (Hayward et al., 2006a; Kingdon, 2013; Winterbach et al., 2013). Studies may also have been limited by the ability of researchers to cost-effectively collect data on the species. Leopards – as wide-ranging, cryptic, and solitary carnivores – are difficult to observe directly (but see Bailey, 2005). Further, the costs of deploying GPS radio collars, a tool commonly used to investigate the ecology of cryptic species (Kays et al., 2015; Wilmers et al., 2015), may have been prohibitively expensive, particularly for such a species that, until relatively recently, was of low conservation priority (Jacobson et al., 2016; Stein et al., 2016). In short, the high costs of acquiring information on leopard intraguild interactions, coupled with the species' low conservation priority, may have led to resources, understandably, being directed towards species with a greater perceived need. Recent advances in GPS technology, however, have reduced the costs of data acquisition (Kays et al., 2015; Wilmers et al., 2015), opening an opportunity to address this knowledge deficit. Further, the leopard's conservation status was recently downgraded to '*vulnerable*' (Stein et al., 2016), thereby increasing the urgency of acquiring ecological knowledge to ensure we can implement effective conservation actions, if necessary.

Table 1: Summary of large predator guild species life history traits and behaviours. ♂ = male, ♂♂ = males, ♀ = female, and ♀♀ = females

Species	Mass (range)	Social structure	Home range size (mean and range)	Foraging and food
Lion (*Panthera leo*)	♂♂: 145.40–225.00 kg [a] ♀♀: 83.00–167.80 kg [a]	Adult ♂♂ can form coalitions of 1–7. ♀♀ found in fission-fusion social structures (prides) of 1–18 ♀ adults plus dependent offspring [b].	Serengeti N.P.: ~200 km^2 (20–500 km^2) [b,c]; Kgaladadi Transfrontier Park: 1,462 km^2 (266–4,532 km^2) [b,d]; this study area: ♂♂ 211.23 km^2 (82.32–343.64 km^2); ♀♀ 159.13 km^2 (82.71–364.93 km^2) [e]	Opportunistic stalk and ambush hunters [c]. Optimum prey weight: 350 kg; preferred prey weight range: 190–550 kg [f].
Spotted hyaena (*Crocuta crocuta*)	♂♂: 48.40–70.00 kg [b] ♀♀: 39.00–81.00 kg [b]	Live in mixed sex matriarchal social groups (clans) (size range: 3–90 members) [g,h].	Ngorongoro Crater: 24 km^2 (9–40 km^2) [h]; Central Namib Desert: 570 km^2 (383–816 km^2) [i]; this study area: 239.28 km2 (176.70–408.62 km^2) [j]	Cursorial hunters, with prey sometimes chased over several kilometres [b]. Preferred prey weight range: 56–182 kg (mode: 102 kg) [k].
Leopard (*Panthera pardus)*	♂♂: 20.00–72.00 kg [b] ♀♀: 17.90–43.00 kg [b]	Both sexes are solitary and come together briefly during periods of copulation [l].	Kruger N.P.: ♂♂ 52.00 km^2 (16.40–96.10 km^2); ♀♀ 16.40 (5.60–29.90 km^2) [l]; Southern Kalahari: ♂♂ 2,104.40 km^2 (standard error: 995.95 km^2); ♀♀ 1,258.50 (SE: 541.50 km^2) [m]; this study area: ♂♂ 112.26 km^2 (77.90–130.60 km^2) [n]; ♀♀ 36.05 km^2 (n = 2, 35.02 and 37.07 km^2) [e].	Stalk and ambush within open habitats [o], and wait and ambush within closed habitats [l]. Optimum prey weight: 23 kg; preferred prey weight range: 10–40 kg [p].
African wild dog (*Lycaon pictus*)	♂♂: 18.00–34.50 kg [b] ♀♀: 19.00–26.50 kg [b]	Obligate social breeders living in mixed sexed packs of 2–44 adults [q]. Average pack size: ~9–10 adults [q].	Mean home range size of 50 packs across several studies was 606 km^2 [b]. Can exceed 2,000 km^2 in prey scarce areas [b]; this study area: 739 km^2 (367–999 km^2) [r].	Cursorial hunters – prey pursued over short distances and at high speeds [s,t]. Optimal prey weight ranges: 16–32kg (mode: 24 kg) and 120–140 kg (mode: 132 kg) [u]
Cheetah (*Acinonyx jubatus*)	♂♂: 28.50–64.00 kg [b] ♀♀: 21.00–43.00 kg [b]	♂♂ can form semi-permanent coalitions of 2–4 [b]; ♀♀ are solitary [b].	Kruger N.P.: ♂♂ 188 km^2 (195–242 km^2); ♀♀ 135 km^2 (102–171 km^2) [v]; Namibian farmlands: ♂♂ 1,436.50 km^2 (119.60–4347.60 km^2); ♀♀ 1,578.06 (553.90–4,024.70 km^2) [w]; this study area: ♂♂ 588.42 (210.46–1,070.03 km^2); ♀♀ 573.99 (275.42–748.90 km^2) [e].	Cursorial hunters – prey pursued over short distances at high speeds [t]. Kill most abundant species within weight range of 23–56 kg (mode: 36kg) [x].

[a] (Smuts et al., 1980), [b] (Kingdon, 2013), [c] ([REF, 1976), [d] (Funston et al., 2001), [e] (K. Rafiq, unpublished data), [f] (Hayward and Kerley, 2005) [g] (Mills and Hofer, 1998), [h] (Höner et al., 2005), [i] (Tilson and Henschel, 1986), [j] (Vitale, 2017), [k] (Hayward, 2006), [l] (Bailey, 2005), [m] (Bothma and Bothma, 2012), [n] (Hubel et al., 2018), [o] (Stander et al., 1997), [p] (Hayward et al., 2006a), [q] (Woodroffe et al., 2004), [r] (Pomilia et al., 2015), [s] (Hubel et al., 2016a), [t] (Hubel et al., 2016b), [u] (Hayward et al., 2006b), [v] (Broomhall et al., 2003), [w] (Marker et al., 2008), [x] (Hayward et al., 2006c)

Leopards show high levels of home range, habitat preference, and dietary overlap with other large African carnivores, suggesting that the potential for intraguild competition is high (Caro and Stoner, 2003). Indeed, within certain areas, lions and spotted hyaenas are together the largest cause of leopard cub mortality (Balme et al., 2013). Most intraguild studies involving leopards have predominantly focussed on their interactions with lions (e.g. Du Preez et al., 2015; Miller et al., 2018). Within productive habitats, at the population level, leopards are unaffected by intraguild competition with lions (Balme et al., 2017b; Miller et al., 2018). In contrast, at the habitat-scale, leopard behaviour and space use is impacted by competitor risk. Leopards are, for example, thought to be particularly susceptible to kleptoparasitism (Caro and Stoner, 2003), and prey caching within trees is thought to have evolved as an adaptation to reduce the loss of kills to competitors (Bailey, 2005; Balme et al., 2017a; Stein et al., 2015). Further, leopards transition into denser habitats when lions are nearby (Du Preez et al., 2015), avoid areas recently occupied by lions (Vanak et al., 2013), and increase vigilance levels when lions are perceived to be in the area (Rafiq, 2016).

Many questions, however, on leopard intraguild interactions remain unanswered. Specifically, leopard intraguild studies have predominantly focussed on their interactions with lions (but see Vanak et al., 2013) even though they are sympatric across much of their African range with three other guild members. We know little of their interactions with these species, despite the fact that aggressive interactions, whose end results include kleptoparasitism, injury, and mortality, have been documented between leopards and all other guild members (Bailey, 2005; Balme et al., 2017a; Creel and Creel, 2002; Kruuk and Turner, 1967; Laurenson, 1994; Schaller, 1976). Whilst leopard-lion interactions are likely to be asymmetrical because of pronounced differences in body mass, differences in competitive mass with other guild members are expected to be less pronounced, and dominance may even shift between encounters as competitor group sizes change. Thus, there likely exists a complex dominance hierarchy that is mediated by the circumstances of encounters, and of which we know little about. Further, many of the studies focussing on leopard intraguild interactions have typically relied on spatio-temporal data with large temporal interludes between spatio-temporal locations (Du Preez et al., 2015; Vanak et al., 2013). Consequently, our ability to quantify intraguild encounter frequencies and the spatial dynamics of encounters has been limited because encounters and behaviours occurring between data points have remained undetected.

Thesis structure and overview

The aim of this thesis is to broaden our understanding of the relationships between leopards and their competitors. As such, within this thesis, I present four chapters of original research on leopard ecology and monitoring, primarily within the framework of carnivore interactions. These chapters are outlined below.

Chapter two investigates large-scale spatio-temporal avoidance between leopards and other large predator guild species. Specifically, I consider whether leopards avoid areas intensively used by dominant guild members by using high-resolution GPS radio collar data collected from sympatric guild species over the same time periods. I then expand upon the activity partitioning work of Cozzi et al. (2012) to look at leopard activity patterns in the context of light availability and competitor avoidance.

Chapter three follows on from the results of *Chapter two* by focussing on direct encounters between leopards and other large predator guild members, specifically lions, wild dogs, and cheetahs. I start by looking at intraguild encounter onsets and consider the impact of imperfect decision making and activity overlaps on the instigation of encounters. I then move on to consider the behavioural outcomes of encounters and how these are mediated by the leopard's ecology and life history.

Chapter four investigates optimal leopard scent marking placements for intraspecific communication. I frame the analyses in the context of boundary and hinterland scent marking strategies and investigate the impacts of roads and home range locations on scent mark placements. Scent marking is thought to be a key component in maintaining social structure and cohesion within spatially dispersed populations, such as the leopards, and so likely plays a key role in mediating intraspecific competitor interactions. This chapter was to be followed with a final data chapter on interspecific eavesdropping within the large predator guild; however, a version of this was instead submitted as a book chapter led by a collaborator and so is not included as a chapter within this thesis.

Chapter five then investigates the potential of citizen-science in monitoring large carnivore densities in Africa. Accurately estimating carnivore densities is a key objective for conservation practitioners because it allows resources to be diverted to the species and areas in most need. Within this chapter, I investigate whether photographs obtained from wildlife tourists could be used to estimate large carnivore densities, and if so, how estimates compare to those derived from commonly used monitoring methods. I compare density estimates derived from tourist-photographs, camera trapping, spoor surveys, and call-in stations against known minimum reference density estimates and compare the costs in implementing each method. These results are then discussed in the broader context of implementing monitoring programs within protected areas globally.

Chapter six synthesises the results of the previous research chapters, discusses the limitations of my work, and considers future lines of research arising from this thesis.

Each research chapter is presented as a manuscript that has been, or is in preparation to be, submitted for peer-review but whose formatting has been largely standardised for this thesis. As such, there may be some unavoidable duplication in content between the chapters, particularly when discussing the study site and system. Throughout these four chapters I also use the term 'we' rather than 'I' because although I led the design, analyses, and writing of each manuscript, each manuscript was produced as part of a collaborative effort with multiple co-authors. For transparency, co-authors are included on the title page of the four research chapters, and their contributions to the manuscript are included at the end of each chapter. All work presented within this thesis was reviewed and approved by Liverpool John Moores University's ethical committee (reference number: CM_KR/2016-7) and Botswana's Department of Wildlife and National Parks (permit number: EWT 8 / 36 / 4 xxxv (31)).

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CHAPTER 2

Don’t mind me? Leopards show limited spatio-temporal partitioning to coexist with other large African predators

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Abstract

Competition is an important structuring force within ecosystems and can impact species distributions, densities, and population dynamics. Understanding the mechanisms facilitating coexistence within species assemblages is a key consideration for conservation as intact assemblages are thought to be a critical component in maintaining full ecosystem function. The African large predator guild represents one of the few remaining functionally intact large predator assemblages on Earth, and as such, represents a unique study system to understand competitive interactions. Yet, relatively little is known of the mechanisms facilitating coexistence between some of its members, particularly leopards (*Panthera pardus*). Here, we use overlapping, high-resolution spatio-temporal activity and GPS data on lions (*Panthera leo*), spotted hyaenas (*Crocuta crocuta*), leopards, African wild dogs (*Lycaon pictus*), and cheetahs (*Acinonyx jubatus*) to consider the role spatio-temporal niche partitioning plays in facilitating coexistence between leopards and other guild members. We found that leopards were largely resilient to the effects of intraguild competition. Specifically, overlaps of areas intensively used by leopards with other guild members were similar across guild species, suggesting that predator avoidance has a limited impact on habitat selection within leopard home ranges, with resource distribution likely playing a greater role. Moreover, we found evidence to support the hypothesis that guild species activity patterns are primarily driven by light availability rather than predator avoidance. Our results suggest that predator avoidance has a limited impact on leopard spatio-temporal niches, with aspects of the leopard's ecology and life-history likely facilitating its ability to thrive in close proximity to competitors. Considered alongside other studies, our results suggest that landscape-level approaches to conservation may be suitable for aiding leopard conservation.

Introduction

Competition is an important structuring force within species assemblages and can impact species distributions (Berger and Gese, 2007), densities (Creel and Creel, 1996) and population dynamics (Chesson and Kuang, 2008). These processes can be impacted through exploitation competition, where species respond to limited resource availability caused by competitor resource use (Sarà et al., 2005). They can also be impacted through interference competition, where resource access is limited directly, during physical confrontations between species, and/or indirectly through the risk or fear of encountering competitors and the costs that may be incurred (Du Preez et al., 2015; Palomares and Caro, 1999; Willems and Hill, 2009). Across many landscapes, risk is heterogeneously distributed in both space and time (Creel et al., 2013; Oriol-Cotterill et al., 2015; Willems and Hill, 2009). Heterogeneity is thought to be a critical component for maintaining coexistence between species (Chesson, 2000), and a species' perception to this landscape of risk influences their movements and activity patterns (e.g. Du Preez et al., 2015; Oriol-Cotterill et al., 2015). Indeed, within some ecosystems, spatial and temporal partitioning are thought to be key components in facilitating coexistence between competitors (Durant, 1998; Hayward & Slotow, 2009).

Understanding the mechanisms facilitating coexistence between sympatric large carnivores is relevant to ecosystem functioning because such species can often provide key ecosystem and economic services that have disproportionally large effects relative to that species' density (Estes et al., 2011; Ripple et al., 2014). These regulatory effects, however, are context-dependent, with species assemblages being one of the key context factors influencing carnivore impact and with intact communities of predators thought to support higher biodiversity (Haswell et al., 2017). Maintaining intact predator assemblages is thus critical in maintaining full ecosystem function (Haswell et al., 2017), and understanding the mechanisms facilitating coexistence within such assemblages is relevant to conservation (Winterbach et al., 2013).

The African large predator guild (hereafter referred to as the large predator guild) is one of the few remaining functionally intact large predator assemblages on Earth and, as such, represents a unique study system to understand coexistence (Dalerum et al., 2009). The large predator guild exhibits intense interspecific competition between its five largest species - lion (*Panthera leo*), spotted hyaena (*Crocuta crocuta*), leopard (*Panthera pardus*), African wild dog (*Lycaon pictus*), and cheetah (*Acinonyx jubatus*). In general, the guild exhibits a size-mediated asymmetrical dominance hierarchy, with the circumstances of encounters (e.g. competitive group size) impacting their outcomes (Cooper, 1991; Lehmann et al., 2016). Relatively little, however, is known of intraguild interactions involving leopards. Whilst there has been an increase in the recent number of leopard intraguild studies, these have typically focussed on competition between leopards and lions (e.g. Du Preez et al., 2015; Miller et al., 2018), despite the fact that they co-occur and compete with other guild members across their African range. As a consequence, relatively little is known of whether there is spatial and/or temporal partitioning between leopards and other guild members (but for leopard-lion interactions see Balme et al., 2017; Miller et al., 2018)

We used high-resolution GPS data collected from radio collars deployed on sympatric lions, spotted hyaenas, leopards, wild dogs, and cheetahs in northern Botswana to investigate spatial and temporal partitioning between leopards and other guild members. First, we tested the hypothesis that the potential for competition between leopards and their competitors, specifically lions, wild dogs, and cheetahs, would be reduced through low levels of spatial overlap in their home range cores (i.e. intensively used areas). Spotted hyaenas were not included within the spatial analyses because of a lack of spatio-temporal overlap in leopard and spotted hyaena GPS data. If competitor risk has an impact on leopard space use at this scale, we predicted that leopards would show significantly lower levels of overlap with lions compared to other guild species. We predicted this because of high mortality risks associated with lion encounters (Bailey, 2005; Balme et al., 2013) and because of higher levels of asymmetry in competitive body mass between leopards and lions than between leopards and other guild members. For example, individual lions are typically several times larger than individual leopards, whilst the competitive asymmetry of leopards with wild dogs is likely to vary depending on the number of wild dog pack members (Kingdon, 2013).

The second set of hypotheses concerned temporal partitioning between leopards and other guild members. We extended the analyses of Cozzi et al. (2012) from the same study system because their study lacked the data to investigate leopard activity patterns, and in this process, we tested two non-mutually exclusive hypotheses: (1) that leopard activity patterns are largely driven by competitor avoidance and (2) that leopard activity patterns are largely driven by light availability. We predicted that under the predator avoidance hypothesis leopards would have lower activity levels when lions are most active because of the risks associated with encounters (Cozzi et al., 2012). We predicted that under the light availability hypothesis, leopard activity would increase in the twilight hours because light levels are low-enough to aid hunting but still high enough to detect prey.

Methods

Study area

The study site covered an area of approximately 2,600 km^2 and was located in northern Botswana in the southern-eastern fringes of the Okavango Delta (Figure 1). The study area included Moremi Game Reserve and two wildlife management areas (NG33/34) that were primarily used for photographic tourism. The landscape was a mosaic of habitat types but was dominated by mopane and acacia woodlands (Broekhuis et al., 2013). Annual precipitation was approximately 450 mm. Rains were typically localised to the wet season, which ran from November until March, with April until October then constituting the dry season (McNutt, 1996). Large carnivore densities within our study area were estimated as 1.90 (95% confidence intervals: 1.30–2.94) lions, 12.70 (8.84–19.03) spotted hyaenas, 4.80 (2.54–11.86) leopards, 2.40 (1.38–5.33) wild dogs, and 0.6 (no confidence intervals provided by study) cheetahs per 100 km^2 (Broekhuis, 2012; Rich, 2016).

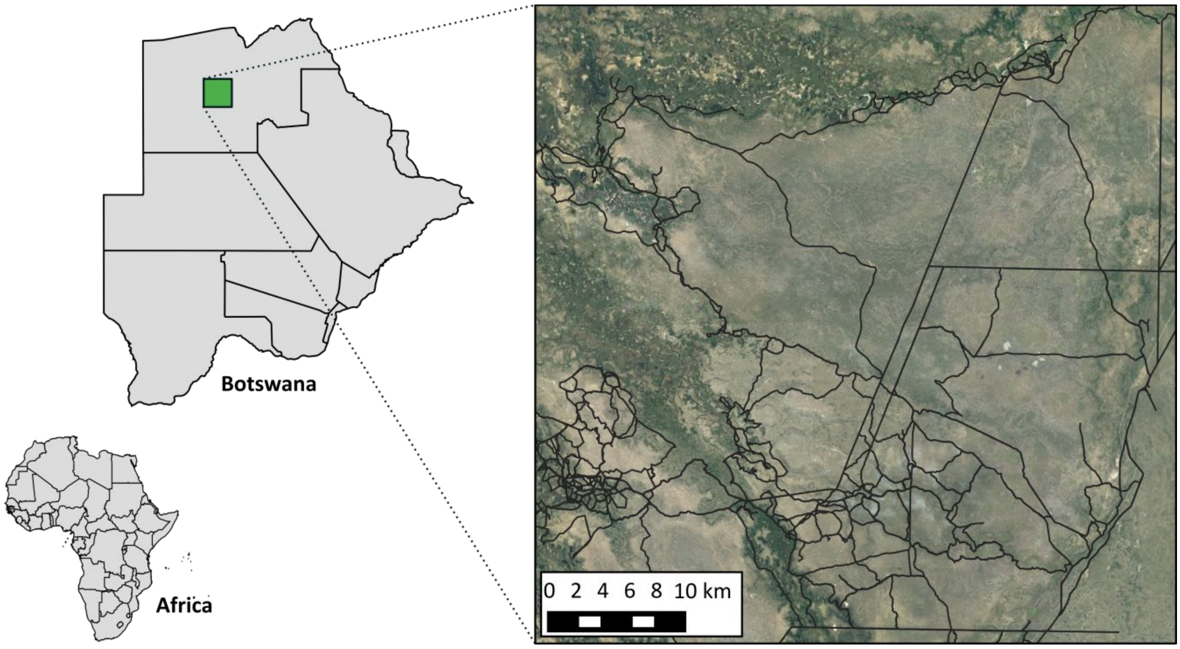

Figure 1: Map of the core study area showing its location within Botswana and Africa. The core study area map was created using Google satellite imagery obtained within the QGIS *OpenLayers Plugin* (Kalberer and Walker, 2018).

Data collection

From November 2011 to January 2018, 26 African wild dogs (from 14 packs), 14 lions (from 4 prides and 3 male coalitions), 8 male leopards, 5 cheetahs, and 1 female spotted hyaena, were fitted with GPS radio collars developed by the Royal Veterinary College (Wilson et al., 2013). Both sexes of lions, wild dogs, and cheetahs were radio collared. We collared only adults of each species to prevent welfare issues that may have arisen with collars tightening following the rapid growth of juveniles. For leopards, adults were determined primarily by their dewlap size (Balme *et al*. 2012), and for the other species, we used a combination of body mass size and the expert knowledge of BPCT researchers to identify adults (Creel and Creel, 2002; Schaller, 1976). Since we selected only mature individuals for collaring, minimal neck growth was to be expected; however, to maximise welfare, we provided two finger widths of space between the individual's neck and collar when tightening attachments. This provided the space required for potential body growth and was of sufficient tightness to prevent collars from prematurely falling off individuals. Radio collars had inertial-measurement-unit activity derived GPS sampling rates, ranging from several fixes per second during periods of high acceleration to hourly fixes during periods of rest (Wilson et al., 2013). Accelerometer data (measured in G-forces, equivalent to 9.8 m/s^2) were also continuously recorded by collars and binned into 30 second windows, with each window having two activity measurements recorded for the X, Y, and Z axes. These measurements were: (1) the largest peak-to-peak acceleration over the 30 second window; and (2) the mean of the mean acceleration values calculated over 15 x two second blocks within the 30 second window (Hubel et al., 2018). For further details on collar specifications see *Wilson et al., 2013*.

Carnivores were initially located through a combination of spoor-tracking, opportunistic sightings, and baited capture sites and were immobilised by a Botswana-registered veterinarian. Immobilisation drug cocktails typically contained two or more of ketamine, medetomidine, xylazine, and Zoletil, depending on the species being immobilised and estimated target weights (see Hubel et al., 2016; Wilson et al., 2018, 2013; Chapter 4). During immobilisations, collar attachment was prioritised and body dimension measurements and biological samples were collected, if viable. During this time, we monitored carnivore vital signs, and we typically completed all work on immobilised individuals within 60 minutes and provided drug reversals, where required, immediately after completion. Collar weights were less than 2% of carnivore body masses and weighed ~970g for lions, ~550g for spotted hyaenas, and ~340g for leopards, cheetahs, and wild dogs. Collars were either removed following expiry or were fitted with a synthetic material or mechanical drop off unit (manufacturer: Sirtrack). All darting activities were approved by Botswana's Department of Wildlife and National Parks. Collar data were available to download via radio link, and animals were visited every two to three weeks by ground vehicle to communicate with collars and check on welfare.

All post-download data processing and statistical analyses were carried out in the R language and environment for statistical computing (R Core Team, 2018).

Core area overlap

We resampled downloaded GPS data to regular inter-fix intervals of 60 minutes and used linear interpolation to assign spatio-temporal coordinates to missing fixes. To avoid pseudoreplication, when multiple lions or wild dogs within the same social group were radio collared over the same time period, we used only the data from the collared animals that had the greatest temporal overlap with leopards. Mean (± standard deviation) data collection days per collar deployment were 356.67 (± 277.80) days for lions; 200.44 (± 111.76) days for cheetahs; 190.90 (± 51.70) days for leopards; 176.89 (± 131.47) days for wild dogs; and 157.00 days for the spotted hyaena. There were three time periods for which we had radio collar data from leopards: April until October 2012, September 2015 until April 2016, and November 2016 until December 2017. This translated to approximately 11, 16, and 37 leopard months of data for each period, respectively, i.e. if three leopards were radio collared over the same two month period, this represented six leopard months of data.

Lion, cheetah, and wild dog data were separated into the three periods that corresponded with leopard radio collar deployments and radio collars that had less than 30 days of temporal overlap with at least one leopard were removed from further analyses to satisfy minimum recommended data points for home range calculation (Seaman et al., 1999). Seasonal kernel utilisation distributions (KUDs) were created for each individual using the $H_{\text{plug-in}}$ bandwidth selection and the resulting 50% isopleth polygon was used to represent areas of intensive use (i.e. core use areas) (Calenge, 2006; Duong, 2017). We applied this method of home range estimation because it has been shown to be one of the most appropriate methods for creating home range utilisation distributions using modern high-resolution telemetry data (Walter et al., 2011). Specifically, it does not result in the over-smoothing of home ranges, as is seen with the creation of KUDs using H_{REF} bandwidth selection. It also provides similar results to more advanced home range estimators, specifically KUDs with least-squares cross validation bandwidth selection and Brownian bridge movement models, whilst being less prone to failure and less computationally intensive (Walter et al., 2011). Seasonal species-level core area maps were then created for each period by merging individual 50% isopleths for each competitor species. This procedure was repeated using 95% isopleths obtained from minimum convex polygons (MCPs) and these were used to exclude data from leopards with low levels of home range overlap with other species. Specifically, leopards with less than 95% overlap of their MCPs with species-level MCPs were removed from this analysis under the assumption that we did not have sufficient GPS data to represent species-level core use areas within that leopard's home range.

Linear mixed-effects models with and without guild species included as the only explanatory variable were used to investigate whether guild species impacted the amounts that leopard core areas overlapped with those of competitors. Due to limited samples when splitting by season, we compared all of the seasons together and included season as a random effect within models. Seasons were defined using historical rain gauge data collected by the Botswana Predator Conservation Trust at the core of the study area. For each year, the wet season was defined as taking place when the first measurable rainfall was recorded in the second half of the year and concluded on the date of the last recorded rainfall in the first half of the following year (i.e. running from approximately November until March). The dry seasons were defined as the remaining months of the year. Leopard identity was also included as a random effect within models to account for repeated sampling of leopards.

An information theoretic approach was then applied to select the most parsimonious model from those with and without guild species included as the explanatory variable. Akaike's Information Criterion corrected for small sample sizes (AIC_C) was used to rank models, with lower values indicating higher levels of support. Models within six AIC_C units of the highest ranked were retained within a candidate set of models in order to ensure a 95% chance of the most parsimonious model being retained (Richards et al., 2011). When multiple models were present within the candidate set, we used multimodel averaging to improve inference through the comparison of individual model parameter estimates (Burnham and Anderson, 2002). Model parameters whose confidence intervals did not encompass zero were interpreted as having a significant impact on the response (Grueber et al., 2011). Since small sample sizes limited our ability to perform statistical analyses on dry and wet season overlaps, we only report mean overlap values for each season. For model specification, selection, and averaging throughout this study, we used the R packages *lme4* and *MuMIn* (Bates et al. 2015; Barton, 2018).

Activity patterns

We used the mean of the mean acceleration values of the X axis (fore-aft direction) as a proxy for activity levels. To investigate the impact of light levels on carnivore activity patterns, we subdivided each day into five periods reflecting the main activity periods within the literature: morning, afternoon, evening twilight, night, and morning twilight (*sensu* Cozzi et al., 2012) (Table 1). Periods were defined using sunlight phases obtained from the R package *suncalc* (Agafonkin and Thieurmel, 2018). To avoid pseudoreplication, we calculated the mean activity values for each period so that there was only one period value per individual per day (Cozzi et al., 2012). The proportion of the moon illuminated and lunar phase were also obtained from the *suncalc* package for each day, and daily mean temperatures for each period were obtained from hourly measurements taken by the Maun Airport meteorological station (location: 23.426, -19.976) (Wolski, 2018).

Table 1: Definitions of the time periods used in our analyses. For our study, we defined the same periods used by Cozzi et al. (2012) and used times specified within the R package *suncalc* (Agafonkin and Thieurmel, 2018).

Period	**Definition**
Morning	Beginning at sunrise, when the edge of the sun appears on the horizon, and ending at solar noon, when the sun is in its highest position.
Afternoon	Beginning at solar noon and ending at the onset of evening civil twilight.
Evening twilight	Beginning when evening civil twilight starts, and ending when it is dark enough for astronomical observations.
Night	Beginning at the end of evening twilight, and ending at the onset of morning nautical twilight.
Morning twilight	Beginning at the onset of morning nautical twilight, and ending at sunrise.

A series of linear mixed-effects models were then specified to test for the impact of nocturnal light levels on carnivore activity. For this, we used only the data that were collected during the dry season since, unlike the wet season, there is limited cloud cover to obscure nocturnal light levels (Cozzi et al., 2012). We specified separate models for each species, with nocturnal activity set as the response variables. Activity levels were transformed using the square root or logarithmic transformations, where necessary, to satisfy assumptions of residual normality. The proportion of the moon illuminated was used as a proxy for nocturnal light levels and was included within models as the explanatory variable; nocturnal activity from the previous day and temperature were included as covariates; and individual identity was included as a random effect (Cozzi et al., 2012). We applied a similar information theoretic approach for model selection as outlined previously to select the most parsimonious model from a series of candidate models derived from all possible permutations of the global, but we used the standard Akaike's Information Criterion (AIC) to rank models.

To easily visualise differences in predator activity with moon illumination, we also grouped and calculated mean activity values across three periods of moon phase: new moon, when < 95% of the lunar disc is visible; half-moon, when 47.5 to 52.5% of the lunar disc is visible; and full moon, where > 95% of the lunar disc is visible.

All presented mean values are reported with the standard error and represent predicted averaged model values.

Results

Home range overlap

Across the three time period categories, there were six leopards that had over 95% of their home ranges overlapping with lion, cheetah, and/or wild dog species-level distributions. There was no overlap between the single radio collared spotted hyaena and any of the radio collared leopards. One leopard had GPS data available across all three time period categories. In this case, data between the periods were considered independent because data from the same seasons were collected in different years. Overall, there was no significant difference in how much leopard core areas overlapped with the core areas of lions (n = 11, 28.23 ± 1.80 %), wild dogs (n = 6, 29.51 ± 2.68 %), or cheetahs (n = 2, 24.25 ± 0.01 %) (Table 2). Similarly, dry season overlaps of leopard core areas with those of lions (n = 8, 24.75 ± 0.06 %), wild dogs (n = 4, 25.28 ± 0.11 %), and cheetahs (n = 2, 24.25 ± 0.01 %) were similar. In the wet season, leopard core areas overlapped slightly more with lions (n = 3, 37.49 ± 0.16 %) and wild dogs (n = 2, 37.97 ± 0.22) than in the dry season, but the overlaps between species within the season were similar.

Table 2: Summary of candidate models (Δ AIC_C < 6) and averaged model parameters from linear mixed-effects models investigating the overlap of leopard core areas with lion, wild dog, and cheetah core areas.

Model	K	R^2	AIC_c	Δ AIC_c	Wi
Null model	4	0.059	5.690	-	0.950
Species	6	-0.279	11.562	5.872	0.050

				Confidence Intervals	
Parameter	**Estimate**	**SE**	**Adj. SE**	**Lower**	**Upper**
(Intercept)	0.306	0.102	0.111	0.089	0.523
Species (lion)	0.006	0.042	0.045	-0.221	0.443
Species (wild dog)	0.011	0.062	0.064	-0.124	0.578

K = degrees of freedom; AIC_C = Akaike's Information Criterion corrected for small sample sizes; Δ AIC_c = difference between this models AIC_C with the lowest AIC_C value out of all models; Wi = Akaike weight. Random effect variable variances (± SD): leopard ID, 0.01 ± 0.08; season, 0.01 ± 0.11.

Activity patterns

All species had high activity levels during morning and evening twilight periods. Leopards, lions, and the spotted hyaena also had relatively high nocturnal activity levels, whilst cheetahs were the only species to show high levels of morning activity (Figure 2). Moonlight illumination had no impact on lion, spotted hyaena, or leopard nocturnal activity levels but did have a positive association with wild dog and cheetah activity (Tables 3–4). Mean lion, spotted hyaena, and leopard nocturnal activity levels were similar across moon phases, but wild dogs and cheetahs were 2.2 and 1.4 times more active, respectively, during full than new moon phases (Figure 3).

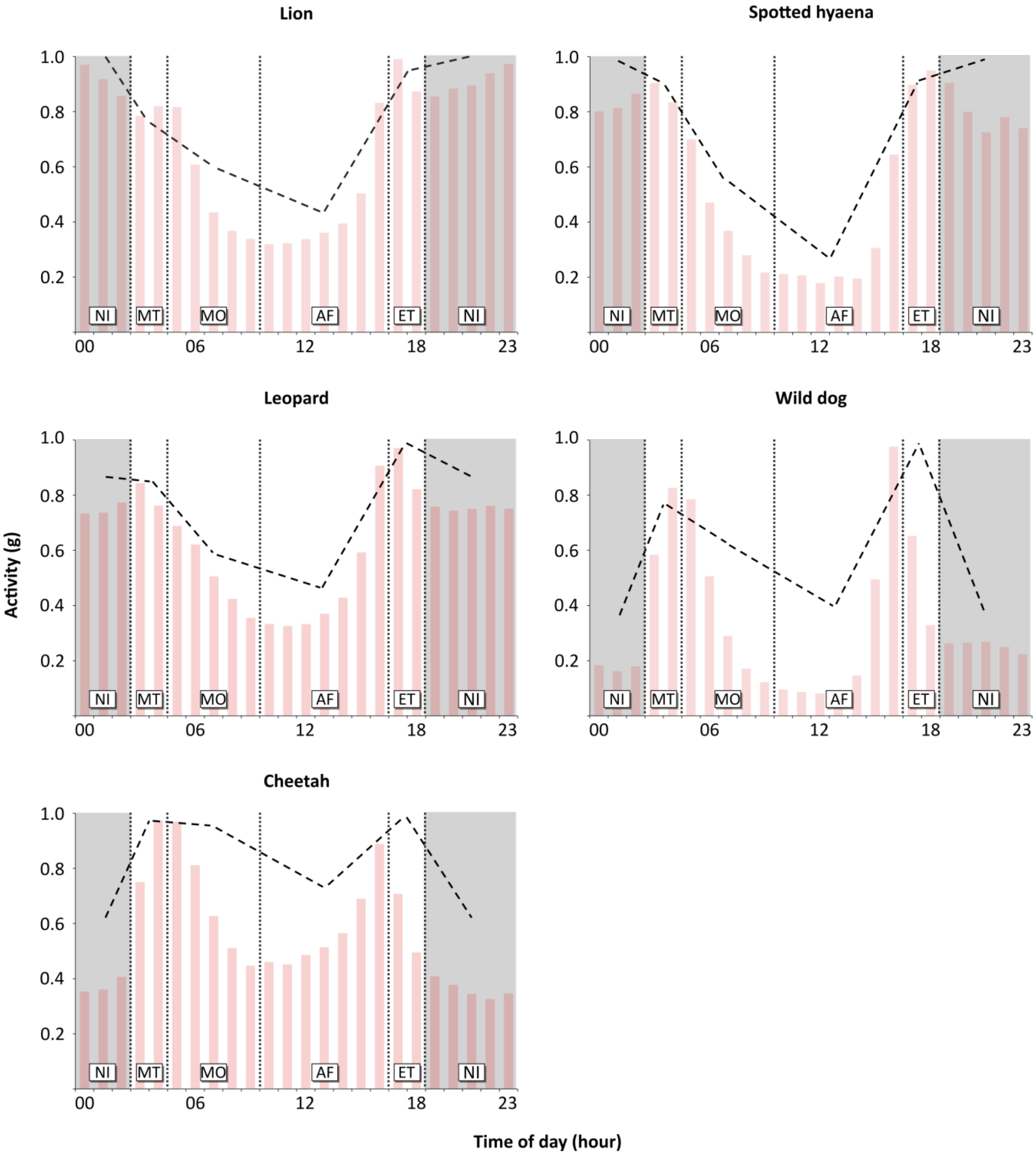

Figure 2: Mean species activity levels for morning twilight (MT), morning (MO), afternoon (AF), evening twilight (ET), and night (NI) diel periods (dashed line). Standard errors are between 0.004 and 0.044 and so cannot be visualised on graphs. The background bar plots shows mean species activity levels blocked into hourly periods. To account for species-level differences in activity values, activity values for each species are standardised against the species' highest activity level across the five periods (dashed) or across the 24 hour blocks (bar plot). Activity values are measured in G-forces (g), equivalent to 9.8 m/s^2.

Table 3: Summary of linear mixed-effects candidate models (Δ AIC < 6) looking at the effect of moonlight illumination on large predator guild species activity levels. Within the models columns, models are grouped by species (bold).

Models	K	R^2	AIC_c	Δ AIC_c	Wi
Lion					
Previous day's activity + moon illumination + temperature	6	0.310	16970.960	-	0.608
Previous day's activity + temperature	5	0.310	16971.830	0.877	0.392
Spotted hyaena					
Previous day's activity	4	0.210	976.579	-	0.527
Previous day's activity + temperature	5	0.211	978.502	1.923	0.201
Previous day's activity + moon illumination	5	0.211	978.543	1.964	0.197
Previous day's activity + moon illumination + temperature	6	0.211	980.476	3.898	0.075
Leopard					
Previous day's activity	4	0.299	4066.616	-	0.501
Previous day's activity + moon illumination	5	0.299	4068.160	1.544	0.231
Previous day's activity + temperature	5	0.299	4068.633	2.016	0.183
Previous day’s activity + moon illumination + temperature	6	0.299	4070.161	3.545	0.085
Wild dog					
Previous day's activity + moon illumination + temperature	6	0.242	13727.270	-	1.000
Cheetah					
Previous day's activity + moon illumination + temperature	6	0.280	2553.024	-	0.817
Previous day's activity + moon illumination	5	0.276	2556.071	3.048	0.178

K = degrees of freedom; AIC_C = Akaike’s Information Criterion corrected for small sample sizes; Δ AIC_c = difference between this models AIC_C with the lowest AIC_C value out of all models; Wi = Akaike weight. Random effect variable variances (± SD): lion ID, 1.422 ± 1.193; leopard ID, 1.307 ± 1.143; spotted hyaena ID, 0.865 ± 0.931; wild dog ID, 1.673 ± 1.293; cheetah ID, 0.241 ± 0.491.

Table 4: Model averaged parameters from linear mixed-effects candidate models (Δ AIC < 6) (specified in Table 3) looking at the effect of moonlight illumination on large predator guild species activity levels. Within the parameters column, parameters are grouped by species (bold). * indicates model parameters with a significant impact on activity levels.

				Confidence Intervals	
Parameters	**Estimate**	**SE**	**Adj. SE**	**Lower**	**Upper**
Lion					
(Intercept)	7.038	0.363	0.364	6.325	7.751
Previous day's activity *	0.017	0.001	0.001	0.015	0.019
Moon illumination	-0.090	0.099	0.099	-0.319	0.023
Temperature *	-0.040	0.007	0.007	-0.053	-0.027
Spotted hyaena					
(Intercept)	10.813	1.143	1.150	8.559	13.068
Previous day's activity *	0.015	0.002	0.002	0.010	0.020
Temperature	-0.006	0.033	0.033	-0.140	0.095
Moon illumination	-0.073	0.357	0.359	-1.542	1.005
Leopard					
(Intercept)	7.873	0.448	0.449	6.993	8.753
Previous day's activity *	0.012	0.002	0.002	0.008	0.016
Moon illumination	-0.039	0.115	0.115	-0.472	0.225
Temperature	0.000	0.009	0.009	-0.034	0.037
Wild dog					
(Intercept)	4.820	0.482	-	3.879	5.763
Moon illumination *	3.602	0.238	-	3.133	4.067
Previous day's activity *	0.009	0.001	-	0.007	0.010
Temperature *	0.086	0.017	-	0.051	0.121
Cheetah					
(Intercept)	2.457	0.276	0.276	1.916	2.998
Previous day's activity *	0.007	0.001	0.001	0.004	0.009
Moon illumination *	0.292	0.082	0.083	0.130	0.453
Temperature *	0.011	0.008	0.008	0.002	0.025

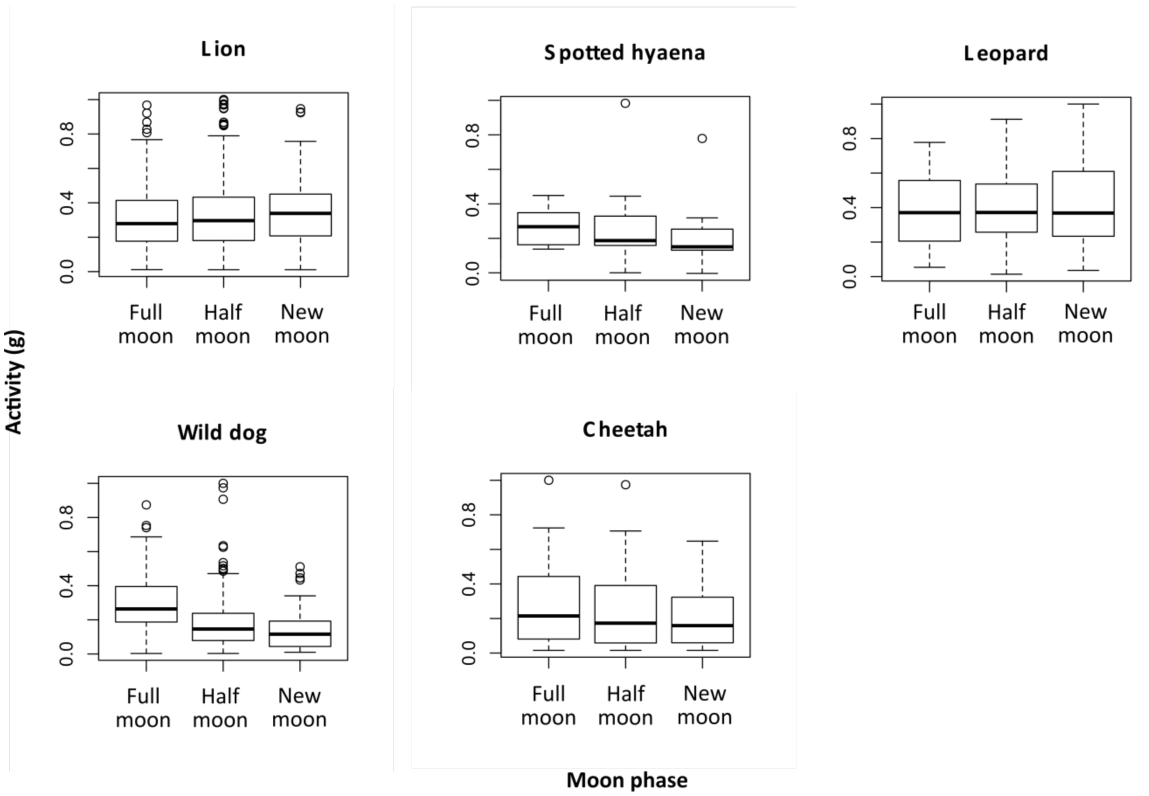

Figure 3: Boxplot of species activity levels across new moon, half moon, and full moon phases. To account for species-level differences in activity values, activity values for each species are standardised against the species' highest activity level across the three phases.

Discussion

Our study revealed no differences in core area overlaps between leopards and different guild species and extensive overlaps in activity patterns between leopards and guild members. As such, our results suggest that, at a population level, leopards are minimally impacted by guild members in terms of broad scale space use and activity but not necessarily behaviour. Leopards showed low levels of spatial overlap in their core use areas with areas intensively used by other guild species but did not completely avoid them. Given that levels of leopard core area overlaps did not significantly differ between guild species despite different levels of risk posed by each, we find it unlikely that competitor avoidance was the primary force driving low levels of spatial overlap. Instead, we speculate that these patterns may reflect species' resource distributions and the selection of different habitat features by each species, likely related to differences in their ecology and life histories. Within similar landscapes to that of our study, leopards, for example, select for intermediately vegetated habitat types associated with high prey densities and prey catchability, independent of lion presence, whilst lions select for open habitats with higher densities of large prey species (Miller et al., 2018). As such, our results fit the hypothesis that within home ranges, leopard space use is driven by resource distribution rather than predator avoidance (Rich et al., 2017), with reactive spatio-temporal behavioural adjustments then perhaps used to mitigate risk (e.g. Broekhuis et al., 2013; Swanson et al., 2016). Although, we acknowledge that this is speculation only, since we had no measure of bottom-up forces within this study.

Interspecific overlap of leopard core areas may reflect locations with habitat features selected for by multiple guild members but where the risks of encounters are mitigated by habitat structure (Janssen et al., 2007). Lions in the Okavango Delta, for example, use woodlands more than expected by chance (Broekhuis et al., 2013), and impala (*Aepyceros melampus*), one of the preferred prey species of leopards and wild dogs (Hayward et al., 2006a; 2006b), prefer woodland habitats over grasslands and floodplains (Bommel et al., 2006). As such, for leopards, occupying shared woodland habitats carries benefits of increased prey densities (Bonyongo, 2005) and prey catchability (Balme et al., 2007), and it also provides leopards with vertical refuge from intraguild conflict (Stein et al., 2015) and conceivably minimises the chances of their detection by competitors. Co-occupation of shared habitat patches may also be facilitated by aspects of the leopard's life-history that, in comparison to some other guild species, make them particularly well suited to co-existence within these areas. Leopards are a cryptic and solitary species and so they may be able to maintain a relatively low risk of detection by dominant competitors whilst moving through shared areas (Bailey, 2005). This is in contrast to wild dogs, for example, whose distance from other pack members when mobile and whose mode of movement (i.e. fanned out and coursing) (Hubel et al., 2016b) may make them predisposed to increased detection and ambush by larger predators. Thus, instead of avoiding all high competitor risk areas, leopards appear to instead adjust aspects of their behaviour when within high risk locations, such as the hoisting of prey into trees (Balme et al., 2017a; Stein et al., 2015).

African large predator guild members also showed high levels of temporal overlap, adding to the growing body of evidence that temporal partitioning plays a limited role in facilitating competitor coexistence (Cozzi et al., 2012; Kronfeld-Schor and Dayan, 2003; Rich et al., 2017). We found that leopard activity levels: (1) peaked during evening twilight; (2) showed extensive temporal overlap with those of lions and the spotted hyaena; and (3) along with lion and spotted hyaena activity levels, showed no association with moonlight availability. In contrast, the largely diurnal cheetahs and primarily crepuscular wild dogs showed positive associations with moonlight availability, reflecting their ocular evolution (Ahnelt and Kolb, 2000).

Finding similar temporal activity patterns, Cozzi et al. (2012) offered hunting strategies as an explanation. For ambush predators, such as lions, low-light conditions increase hunting success (Funston et al., 2001; Packer et al., 2011), and therefore, nocturnal activity levels may remain consistent across moon phases due to the need to meet minimum energetic requirements and the limited hunting opportunities available across other diel periods. In contrast, for cursorial hunters, such as cheetahs and wild dogs, increased light levels may provide advantages in maintaining visual contact with targets and reducing injury risks whilst chasing prey (Cozzi et al., 2012), with foraging in nocturnal light providing the additional advantage of allowing hunters to approach closer to prey without being seen (Rasmussen and Macdonald, 2012). Thus, wild dogs and cheetahs may preferentially engage in more nocturnal foraging behaviours during lunar phases when hunting success is increased but, unlike ambush predators, otherwise be capable of meeting their energetic requirements during other diel periods, i.e. when the costs of nocturnal hunting outweigh the benefits (Cozzi et al., 2012; Creel and Creel, 2002). Whilst this hunting strategy explanation may also account for leopard diel activity patterns, it does not explain why spotted hyaenas, which are also cursorial predators, do not have a positive association between moonlight availability and nocturnal activity levels. Instead, evidence is accumulating that thermoregulatory limitations restrict their diurnal activity (Hayward and Hayward, 2007). Ultimately, as with space use, temporal activity patterns likely arise from a complex interplay between different life-history trade-offs (e.g. hunting and territorial maintenance requirements), with the niche of these guild members partitioned across multiple axes to enable coexistence. As such, in the context of our hypothesis, carnivore activity is likely a function of both competitor activity and light availability, albeit to potentially differing degrees.

Our results suggest that top-down effects are not always a predominant regulatory force within intact ecosystems, as is commonly suggested (Terborgh, 2010). Leopards successfully coexist amidst the highly competitive African large predator guild despite exhibiting low spatial and no temporal avoidance – in general, at the population level they seem utterly unfazed by competitors (Balme et al., 2017; Miller et al., 2018).

Thus, we found little evidence that interactions between leopards and other guild members can be understood within the mesopredator release framework, i.e. one of top-down suppression by dominant competitors (Allen et al., 2017; Miller et al., 2018). This provides a glimpse into the regulatory structure within a functionally intact predator guild whose baseline interactions are unlikely to have been impacted by megafauna extinctions, and our results provide strong evidence that top-down regulation between dominant and subordinate competitors is not universal. Instead, the strength of top-down regulation is likely to be species- and population- specific and dependent on a number of environmental factors, such as resource availability, habitat structure and prey range (Carbone et al., 1997; Haswell et al., 2017; Swanson et al., 2016). Currently, the vast majority of evidence of mesopredator suppression and release in the terrestrial realm come from guilds that were devastated by Pleistocene extinctions, such that their modern ecological simplicity (i.e., few trophic levels and apex predators) may mean that they no longer reflect the conditions within which they evolved (Allen et al., 2017).

In summary, we have shown that leopard spatio-temporal niches are minimally impacted by predator avoidance, and instead we speculate, may be primarily driven by resource acquisition. Our results suggest that leopards within relatively undisturbed ecosystems, with relatively high productivity, can coexist alongside competitors with minimal impacts. As such, our study supports the idea that a landscape-level approach to conservation, wherein conservation strategies focus on healthy landscapes with the capacity to carry multiple species (Sanderson et al., 2002), may be suitable for conserving leopard populations (Miller et al., 2018). That said, in the absence of large scale spatial or temporal avoidance of competitors, it is likely that leopards adapt fine-scale behaviours to perceived competitor risk or during the occurrence of direct competitor encounters; however, beyond prey caching (Balme et al., 2017a; Stein et al., 2015), little is known of these coexistence mechanisms. Further, it is also unknown how high levels of niche overlap impact competitor risk and competitive dynamics, e.g. their impact on guild member encounter frequencies. Whilst such intraguild interactions were beyond the scope of this study, investigations into fine-scale coexistence mechanisms will provide greater insights into the factors allowing leopards to coexist within such a highly competitive predator assemblage.

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Author contributions

KR, NJ, and KG conceived the study; KR collected the majority of the leopard data (with other data provided by the BPCT), carried out the analyses, and wrote the manuscript; KG, CM, MH, and NJ contributed to manuscript revisions. AW provided radio collars for the project. JM provided the research infrastructure for field data collection.

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CHAPTER 3

Imperfect decision making and temporal activity overlap contribute to direct encounters between large African predators

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Abstract

Encounters between individuals can have implications for a range of processes, including disease transmission, information transfer, and competition. For large carnivores, difficulties in directly observing individuals and historical hardware limitations of radio collars mean that relatively little is known of the drivers and spatial dynamics of direct encounters. The African large carnivore guild represents one of the few remaining functionally intact guilds of large carnivores on Earth and so represents a unique study system for understanding competitor interactions. Here, we use custom-developed, high-resolution GPS radio collars to investigate direct encounters amongst some of its members. Specifically, we investigate encounter onsets and dynamics for leopard (*Panthera pardus*) encounters with lions *(Panthera leo*), African wild dogs (*Lycaon jubatus*), and cheetahs (*Acinonyx jubatus*). We found that encounters were instigated by all species, but leopard instigated encounters with (likely) competitively dominant species appeared to reflect imperfect decision making, primarily occurring within habitats with limited visibility. Moreover, encounters peaked during periods of high temporal overlap, suggesting that although temporal activity patterns may not be driven by predator avoidance, they have implications for competitor dynamics. Leopards, however, were relatively resilient to the effects of intraguild competition, with limited or no changes in behaviours and movements following encounters. Considered alongside other studies, our results indicate that despite high levels of interference competition and spatio-temporal overlap with other large predators, leopards are able to coexist alongside competitors with minimal costs. Our results show how habitat characteristics and niche overlaps contribute to encounters between competitors and provide an example of how considering the factors driving encounters and the costs of encounters can help inform on the consequences of shifting environments.

Introduction

Encounters between individuals of free-ranging species are important to understand because they inform a range of ecological processes, including disease transmission (Craft et al., 2011), information transfer (Berger et al., 2001), and competition (Jordan et al., 2017; Macdonald, 2016). Within this context, large carnivore species can be a special case in point since they often help to regulate and structure ecosystems (Ripple et al., 2014). Large carnivore impacts are context dependent and exist within a network of interactions which together structure communities (Haswell et al., 2017). Encounters amongst members of large carnivore assemblages can thus have cascading effects throughout lower trophic levels because encounters can impact species population dynamics, distributions, densities, and behaviours (Berger and Gese, 2007; Elbroch et al., 2014; Groom et al., 2017).

Carnivore interactions have typically been studied at the home range and landscape levels (Miller et al., 2018; Rich et al., 2017), and resource partitioning across different niche axes as a mechanism for carnivore coexistence has been well documented (Kamler et al., 2012; Karanth et al., 2017; Steinmetz et al., 2013). However, relatively little is known of direct encounters between species and of the impact that population-level niche partitioning may have on encounter rates and behaviours at a local scale. This is important to understand because species often show a degree of plasticity that allows them to shift their positions along niche-axes in response to fluctuating environments (Kitchen et al., 2000; Kronfeld-Schor and Dayan, 2003), and such shifts could conceivably impact encounter rates and intraguild competition dynamics.

Encounters between large carnivores have traditionally been difficult to study because these species typically occur at low-densities, are wide-ranging, and move over landscapes that are logistically difficult for researchers to navigate (Gittleman, 2001). To overcome these challenges, GPS radio collars have historically been used to study large carnivore ecology (Wilmers et al., 2015). These too, however, have been ill-suited in their ability to quantify interactions because hardware limitations inhibited their ability to collect fine-scale GPS data, meaning that encounters could go undetected between data points (Du Preez et al., 2015). Further, whilst animal borne proximity loggers have increasingly been used to record animal contacts, the proximity data collected frequently lacks the GPS data required to provide ecological context and assess encounter outcomes (Ossi et al., 2016; Rutz et al., 2015). Thus, much of what we do know of direct large carnivore interactions is typically based on opportunistic sightings from ground-vehicles (e.g. Bailey, 2005; Schaller, 1976) and from intensive-monitoring of select areas of interest, such as kill sites, *via* camera traps (e.g. Selva et al., 2003). Whilst useful, such data is often qualitative and captured over short spatio-temporal scales, which limits our ability to make inferences on the wider consequences of encounters for species behaviours and space-use. Further, such data is commonly biased towards landscapes suited to opportunistic sightings, such as the short grasslands of the Serengeti (Schaller, 1976). Habitat structure can, however, change the dynamics of interspecific encounters (Bailey, 2005; Janssen et al., 2007), and so the occurrence and consequences of encounters within landscapes less suited to opportunistic sightings should also be considered. Recent advances in GPS radio collar operational times and sampling frequencies (< 5 minute GPS fix intervals) offer an opportunity to address these limitations and to provide exhaustive GPS monitoring that captures interactions that previously would have been missed (Jordan et al., 2017). Although, radio collars are being increasingly used to quantify direct interactions in other taxa (e.g. Crofoot, 2013), their application to large carnivore interactions has thus far been limited (but see Elbroch and Quigley, 2017; Jordan et al., 2017).

In this study, we investigated intraguild encounters between four members of Africa's large predator guild: lion (*Panthera leo*), leopard (*Panthera pardus*), African wild dog (*Lycaon pictus*), and cheetah (*Acinonyx jubatus*). These species are members of one of the last intact guilds of large carnivores on the planet and, as such, represent a unique baseline study system to investigate interspecific encounters within a functionally intact group (Dalerum et al., 2009). Leopards are a solitary large felid that coexist across much of their sub-Saharan range with other guild members (Jacobson et al., 2016; Kingdon, 2013). Despite this, they are arguably one of the least studied guild species in terms of intraguild interactions. Further, although there is intense interspecific competition within the guild and the population-level outcomes of encounters have been well studied (e.g. Groom et al., 2017; Miller et al., 2018; Swanson et al., 2014), relatively little is known of the factors leading to and the spatial dynamics of intraguild encounters, particularly those involving the leopard.

We used custom-developed high-resolution GPS radio collars to investigate encounter onsets and spatial dynamics between leopards and other large predator guild members within northern-Botswana. We hypothesised that encounters between guild members are the result of imperfect decision making rather than omniscient knowledge of competitor risk. In particular, we investigated the role habitat structure may play in imperfect decision making because although it can facilitate coexistence between competitors (Janssen et al., 2007), it can also impact information transfer (Boncoraglio and Saino, 2007) and relatively little is known of its impact on decision making. Under this imperfect decision making hypothesis, we predicted that encounters instigated by the movements of smaller competitors would occur primarily within closed than open habitat types, i.e. where visual information, the best indicator of an animal's exact location, on competitors is harder to acquire and the chances of stumbling into competitors is greater.

We then investigated the temporal circumstances under which encounters occurred, paying particular consideration to the consequences of reduced temporal partitioning on encounter frequencies (Chapter 2). We hypothesised that encounters across the diel cycle would occur most often during periods of high activity overlap between dyad members because guild members: (1) often compete for similar resources and thus are likely to be attracted to similar areas during periods of movement (Caro and Stoner, 2003; Hayward and Kerley, 2008), (2) may preferentially use the same landscape features (e.g. roads) as travel routes (Abrahms et al., 2016), and (3) during certain life history periods may occupy non-favourable habitats during periods of rest (Groom et al., 2017). We also predicted that leopard-wild dog and leopard-cheetah nocturnal encounters would peak during periods of high illumination because wild dog and cheetah nocturnal activity levels are positively associated with light availability, but we predicted that, conversely, leopard-lion encounters would not (Cozzi et al., 2012; Chapter 2).

Finally, we sought to investigate the impact of competitor encounters on leopard behaviours and movements. We hypothesised that the scale and response to encounters would depend on the species met and characteristics of the habitat within which encounters occurred. Specifically, we predicted that within open habitats, leopards would increase step lengths, reduce path tortuosity, and transition from stationary to moving behaviours in order to assist a flee response from lions and wild dogs. Within closed habitats we hypothesised that habitat structure would facilitate crypsis and provide vertical refuge (Bailey, 2005; Balme et al., 2007). Thus, we predicted that within closed habitats, leopards would favour the opposite responses from open habitats during lion and wild dog encounters. For lions, these predictions were based on the costs lions impose upon leopards through mortality, injuries, and kleptoparasitism (Bailey, 2005; Balme et al., 2017a, 2017b; Schaller, 1976). In contrast, antagonistic interactions between leopards and wild dogs are more likely to occur in both directions (Bailey, 2005; Creel and Creel, 2002). However, given the numerical advantage and larger relative competitive mass of wild dog packs, we expected that wild dogs would more often pose a risk to leopards and, thus, would elicit similar leopard responses as during lion encounters. In contrast, we hypothesised that leopard encounters with cheetahs would have minimal impacts on leopard behaviours and movements because of limited evidence within the literature of harassment of leopards by cheetahs.

Methods

Study area

This study took place in the Ngamiland region of northern Botswana and covered an area of approximately 2,600 km^2 (centre: -19°51’S, 23°65’E), whose main habitat types were woodlands dominated by acacia and mopane species (Broekhuis et al., 2013). The study area included two wildlife management areas, NG33 and NG34, primarily used for wildlife tourism throughout the study period (November 2011 to January 2018), and areas of Moremi Game Reserve.

Radio collars

For this study, we used GPS radio collars fitted with GPS-linked inertial measurement units (GPS-IMU) that were developed by the Royal Veterinary College, University of

London (Wilson et al., 2013). To conserve battery life and maximise collar deployment, collars switched between different sampling regimes based on GPS-IMU activity-derived behaviour classifications. Specifically, during periods of high acceleration, several fixes per second were recorded; during periods of other locomotion, fixes were recorded every five minutes; and hourly fixes were recorded during periods of inactivity. Data were stored onto a 2GB SD flash card and were downloaded to a ground vehicle *via* radio link every two to three weeks, or thereafter as soon as possible. Further details on collar development and specifications can be found in Wilson et al., 2013.

To fit collars, immobilisations were carried out by a Botswana-registered veterinarian after animals were located through spoor tracking, opportunistic sightings, and/or the use of baited capture sites. Immobilisation cocktails were typically delivered *via* an air-pressure powered dart gun (TELINJECT) with drug combinations and quantities varying with species and individual mass and determined by the veterinarian (see Hubel et al., 2016; Wilson et al., 2018, 2013; Chapter 4). Collar weights for lions (~970g), leopards, wild dogs, and cheetahs (~340g) represented < 2% of collared animal body masses. Collars were typically fitted with bio-degradable or electronic (manufacturer: Sirtrack) drop-off units, and collars with no drop-off unit were manually removed from animals following the completion of the study or upon collar expiry. Carnivore vital signs were monitored throughout immobilisations, and we prioritised collar attachment over body measurement and biological sample collection. Most immobilisations were concluded within 60 minutes and reversal drugs were administered intramuscularly. Animals were then monitored from a ground-vehicle until drug side-effects appeared to have worn off, i.e. animal movements and coordination returned to pre-immobilisation levels. In total, we immobilised and radio collared 14 lions, 8 leopards, 26 African wild dogs, and 5 cheetahs. For details on selection and collaring of animals, see Chapter 2. We had radio collar data for male and female lions, wild dogs, and cheetahs and radio collar data for male leopards. Mean collar deployments were 356.67 (± 277.80, standard deviation) days for lions, 190.90 (± 51.70) days for leopards, 176.89 (± 131.47) days for wild dogs, and 200.44 (± 111.76) days for cheetahs.

Encounter identification

To identify encounters, raw datasets were resampled to create regular trajectories of fixes at one minute intervals through a combination of linear interpolation and down sampling of high-resolution GPS data within the R environment for statistical computing (R Core Team, 2018). To filter erroneous GPS locations from our dataset, prior to interpolation, we removed GPS fixes with < 15 m horizontal accuracy and removed fixes that required individuals to have travelled at speeds exceeding 15 m/s between locations > five minutes apart. Although large African predators can reach maximum speeds that exceed these values, these speeds typically occur over short distances and are unlikely to have been sustained over five minute step lengths (Hubel et al., 2018; Wilson et al., 2013).

Leopard-competitor (i.e. lion, wild dog, or cheetah) dyads that showed temporal overlap in collar deployments were then cross-referenced to find encounters using the *wildlifeDI* package in R (Long, 2014). Encounters were defined as occurring when simultaneous fixes from dyad members were within 200 m of one another. This 200 m threshold was a conservative measure of the distance leopards may directly detect competitors within woodland habitats (Rafiq, 2016). The temporal threshold for defining fixes as simultaneous was set at ½ of the iterated sampling intensity, i.e. fixes within 30 seconds of one another were defined as simultaneous. The encounter location and encounter time were defined as the mid-point between the encountering individuals' GPS locations when species were at their closest and the time that this occurred. The encounter area was defined by a 100 m radius (half of the 200 m threshold) around the encounter location. New encounters could not occur until dyad members had vacated the encounter area and had been separated by > 200 m for at least 24 hours since their last encounter (Elbroch and Quigley, 2017). Interpolated GPS locations one hour either side of the encounter time were retained for analyses.

Encounter rates

We used a subset of our data, from 2012 to 2016, to calculate encounter rates. This is when we had the most lion, wild dog, and cheetah radio collars deployed that overlapped spatially and temporally with radio collared leopards. We calculated an adjusted measure of encounter rates to account for the fact that not all individuals of each competitor species within the study area were radio collared. To do this, we first estimated mean monthly encounter rates within leopard-competitor dyads for the months of temporal overlap. These encounter rates were then adjusted by considering the proportion of individuals we had radio collared within the leopard's home range against the estimated densities of each species within the same area. We used reference density estimates specified in *Chapter five* and Broekhuis (2012) to calculate the expected number of individuals for each species within the home range of each leopard. Home ranges were defined as the 95% isopleths from kernel utilisation distributions created using the $H_{\text{plug-in}}$ bandwidth selection. We then multiplied home range density estimates by the number of months that each leopard was radio collared to give an estimated total number of potential leopard-competitor overlap months. For example, if a leopard was radio collared for two months and the density of lions within its home range was four, then this meant that there were eight potential leopard-lion overlap months, i.e. the total number of sample months if all lions within the leopard's home range had been radio collared. We also calculated the actual number of months that each leopard overlapped with each individual competitor for their collar deployments. However, since not all of the competitor's time was spent within the leopard's home range, for each competitor, we multiplied overlapping months by the proportion of their fixes within the leopard's home range. This was repeated for all individuals within a species and the values summed together to create an estimate of the actual amount of leopard-species collar months that we had data for. We then used these values alongside the baseline monthly encounter rate to estimate encounter rates for each species that accounted for the individuals that we did not have radio collared within the population following:

$$\frac{E}{T_C} x \; \frac{D_{HR} \; x \; T_C}{S_A}$$

where E is the total number of leopard-species encounters; T_C is the number of months a leopard was radio collared; D_{HR} is the estimated number of individuals of the competitor species within the leopard's home range; and S_A is the overlapping leopard-species radio collar months.

Classification of habitat types

Encounters were manually classified into open and closed habitat types based on relative canopy cover at each encounter location using Google satellite imagery from the OpenLayers plugin (Kalberer and Walker, 2018) within QGIS (QGIS Development Team, 2018). Specifically, a 100 metre circular buffer was applied to the encounter location and encounters were classified into open habitats, with little to no canopy cover, and closed habitats, with at least 50 % of the area covered by canopies separated by < 5 m. Canopy cover could be clearly identified within the satellite imagery, and so classifications into these broad habitat types were relatively simple.

Encounter Instigation

For each encounter, we recorded the timings that dyad members arrived into the encounter area. If members arrived within 30 seconds of one another, they were assumed to have arrived simultaneously; otherwise, we assumed that the second species arriving into the encounter area instigated the encounter. We then used a series of Fisher's exact tests to investigate counts of leopard and competitor instigated encounters across competitor species and habitat types. We used the R package *suncalc* (Agafonkin and Thieurmel, 2018) to derive moonlight illumination levels and lunar phases for the day of each encounter, and we used a series of Kuiper's one sample tests for uniformity of circular data (Jammalamadaka and Sengupta, 2011) to assess whether leopard and competitor instigated encounters were equally distributed across diel and lunar cycles. We also used graphical displays to make descriptive inferences of the impact of moonlight illumination on encounter onsets. When considering distributions of encounters across lunar cycles and moonlight illumination levels, we used a subset of our data that contained only encounters occurring during the night, which we defined as the period after the day's end of evening civil twilight and before the start of the following day's morning nautical twilight.

Behavioural transitions

We calculated step lengths (Euclidean distance between successive fixes) between interpolated GPS locations and used a topology-based classification approach to classify step lengths < 1 m as stationary behaviours and those > 1 m as locomotory behaviours (Edelhoff et al., 2016). This threshold was chosen after initial exploratory analyses revealed a high frequency of step lengths < 1 m followed by a clear drop in frequency of > 1 m step lengths (Figure S1). As such, we interpreted < 1 m steps to represent stationary periods, with measurement errors contributing to step lengths exceeding zero. We used these behaviours to provide broad activity classifications for the 15 minute periods leading to and following encounters by considering the dominant activities within each period. We then recorded whether leopard behavioural states changed following encounters and the direction of the change, and we used a series of Fisher's exact tests to compare leopard behavioural transitions following encounters with each of the competitor species across open and closed habitats.

Encounter duration, first passage times, and path metrics

For each encounter, we calculated encounter duration (the time dyad members were within 200 m of one another) and for each encounter species calculated first passage times (the time elapsed since encounter start before leaving the encounter area), step lengths, encounter site distances, and path tortuosity. We estimated mean step lengths and path tortuosity across four 15 minute windows after encounters had started, and we estimated encounter site distances 15 and 60 minutes after encounter onsets. We defined encounter site distance as the Euclidean distance between the relocation closest to the encounter site and the final relocation within that period. Tortuosity was defined as the Euclidean distance between the first and final locations within the series over the sum of all series step lengths (Edelhoff et al., 2016). As such, tortuosity was represented as a ratio, with higher values indicating less tortuous paths. Mean step length, encounter site distance, and path tortuosity metrics were also calculated for the same time periods using interpolated data (as above) from exactly 48 hours before encounters, as controls. We chose this 48 hour period since extrinsic factors, such as moonlight illumination and seasonal effects, were likely to have remained similar to encounters, but yet, there was a large enough temporal gap to assume independence between controls and encounters.

We then modelled each of these responses separately for leopards and competitors through a series of linear mixed-effects models. For path metrics and encounter site distances, separate models were constructed for lion, wild dog and cheetah encounters because the limited number of encounters observed for some species constrained the total number of terms that could be included within models. Thus, modelling encounters with each species separately allowed us to explore the potential impacts of additional variables and their interactions on the responses of those species encountered most frequently. As an example, when considering mean step lengths during encounters we had two sets of leopard-lion, leopard-wild dog, and leopard-cheetah models: one modelling leopard step lengths and one modelling competitor step lengths. For first passage times and encounter duration models, competitor species was instead included as a fixed effect, because of a limited number of terms to be included within models (see Table 1). For each leopard-competitor dyad, we also constructed an additional series of models to investigate how leopard/competitor step lengths changed with competitor/leopard proximity. To do this, for each encounter, we binned distances to other dyad members into 200 m windows, up to 1,000 m, and for each 200 m window calculated mean step lengths. These means were then used as responses in models (Table 1). To satisfy assumptions of residual normality, where necessary, response variables of our models were transformed using square root or logarithmic transformations.

Our models contained a mixture of the following terms: habitat type (habitat), competitor species (species), whether values were from encounter or 48 hour control periods (treatment), window since encounter onset (time), and interactions between treatment, habitat, and time (Table 1). Leopard, competitor, and encounter IDs were included within all models as random effects to account for repeated sampling from the same individuals and encounters (i.e. control and actual encounters).

Table 1: Summary of all fixed terms specified in linear mixed-effects models investigating first passage times, encounter durations, step lengths, path tortuosity, and Euclidean distances from encounter sites. All models include leopard, competitor, and encounter ID as random effects.

Response variables	#	Fixed model terms
First passage times for leopards and competitors	1	Species + habitat
	2	Species
	3	Habitat
	4	(no terms)
Encounter durations for leopards and competitors	1	Species + habitat
	2	Species
	3	Habitat
	4	(no terms)
Step lengths and path tortuosity for members of leopard-lion and leopard-wild dog dyads	1	Treatment + time + habitat + treatment x time + treatment x habitat
	2	Treatment + time + treatment x time
	3	Treatment + habitat + treatment x habitat
	4	Treatment
	5	Null
Step lengths and path tortuosity for members of leopard-cheetah dyads	1	Treatment + time + treatment x time
	2	Treatment
	3	Null
Encounter site distances 15 & 60 minutes post-encounter for members of leopard-lion and leopard-wild dog dyads	1	Treatment + habitat + treatment x habitat
	2	Treatment
	3	Null
Encounter site distances 15 & 60 minutes post-encounter for members of leopard-cheetah dyads	1	Treatment
	2	Null
Step lengths with leopard/competitor proximity	1	Species + distance + species x distance
	2	Species + distance
	3	Species
	4	Distance
	5	Null

For each response, models were then ranked against one another using Akaike's information criterion for small sample sizes (AIC_C) (Burnham and Anderson, 2002). All models < six AIC_C units of the best supported were retained within a candidate dataset that was used to estimate model parameters through model averaging (Richards et al., 2011). Model parameters were interpreted as having a significant impact on the response if their confidence intervals did not encompass zero (Grueber et al., 2011). When discussing the mean values associated with modelled responses, we present model averaged values, i.e. those derived from weighted average parameter values (Burnham and Anderson, 2002). Model specification, selection, and averaging were carried out in the R environment for statistical computing and used a combination of the R packages *lme4* and *MuMIn* (Bates et al. 2015; Barton, 2018).

Results

Overview and encounter rates

In total, we recorded 115 leopard-competitor encounters. Specifically, leopards encountered radio collared lions 64 times, wild dogs 43 times and cheetahs 8 times. For each competitor species, after adjusting for only a portion of their populations being radio collared, this translated to 9.01 ± 1.38 leopard-lion, 2.27 ± 0.73 leopard-cheetah, and 2.16 ± 0.54 leopard-wild dog encounters per leopard per month (mean ± standard error).

Encounter instigation

There were only two instances where species arrived into encounter areas at the same time, which may represent random encounters when dyad members were both moving. Overall, all species were as likely to instigate encounters by approaching leopards first, with or without intent, as leopards were to instigate encounters with them (Fisher's-exact test, p = 0.555) (Table 2).

Leopards were less likely to instigate lion encounters within open than closed habitats (Fisher's exact test, p = 0.037). In contrast, leopard-wild dog (Fisher's exact test, p = 0.060) and leopard-cheetah (Fisher's exact test, p = 1.00) encounters were instigated equally by both dyad member species within both habitat types. All five leopard-wild dog encounters within open habitats were, however, instigated by wild dogs, and so rejection of the alternate hypothesis may be due to low samples sizes rather than lack of an effect (Table 2).

Table 2: Summary of leopard and competitor instigated encounters across open and closed habitats

	Open habitat		**Closed habitat**		
Dyad	**Leopard instigated**	**Competitor instigated**	**Leopard instigated**	**Competitor instigated**	**Total**
Leopard-lion	1	9	25	28	63
Leopard- wild dog	0	5	18	19	42
Leopard-cheetah	1	1	4	2	8
Total	2	15	47	49	113

Overall, leopard-lion encounters were non-uniformly distributed across the diel cycle, with encounters typically occurring during the night (Kuiper test statistic (k) = 3.056, p < 0.01). This was also the case when considering lion (k = 2.385, p < 0.01) and leopard (k = 2.321, p < 0.01) instigated encounters separately (Figure 1a). Across the lunar cycle, overall, leopard-lion encounters were uniformly distributed (k = 0.976, p > 0.15), as were those encounters specifically instigated by lions (k = 0.942, p > 0.15) and those instigated by leopards (k = 1.360, p > 0.15). Encounters did, however, appear non-random in respect to nocturnal light levels and, independent of the instigating species, peaked during periods of high moonlight. Interestingly, lion instigated encounters also showed an additional peak during periods of low moonlight (Figure 1b).

Leopard-wild dog encounters, overall, peaked during early evening and late morning hours ($k = 2.124$, $p < 0.01$). For leopard instigated wild dog encounters, there was no significant difference in the distribution of encounters across the diel cycle ($k = 1.586$, $p > 0.10$); in contrast, wild dog instigated encounters peaked in the early morning ($k = 2.722$, $p < 0.01$) (Figure 1c). Overall, leopard-wild dog encounters were uniformly distributed across lunar phases ($k = 0.805$, $p > 0.15$) and so were those encounters specifically instigated by leopards ($k = 0.936$, $p > 0.15$) and by wild dogs ($k = 0.753$, $p > 0.15$). In respect to nocturnal light levels, leopard-wild dog encounters peaked during periods of high moonlight, regardless of which species instigated the encounter. There was also a second smaller peak in encounters during periods of low moonlight when considering leopard and wild dog instigated encounters together (Figure 1d).

Leopard-cheetah encounters most occurred in the early evenings and late mornings ($k = 1.973$ $p < 0.025$). Encounters were uniformly distributed across lunar phases ($k = 0.911$ $p > 0.15$), but did appear to peak during periods of intermediate nocturnal light availability (Figure 1f). Due to a limited leopard-cheetah encounters sample size ($n = 8$), we did not investigate leopard and cheetah instigated encounters separately.

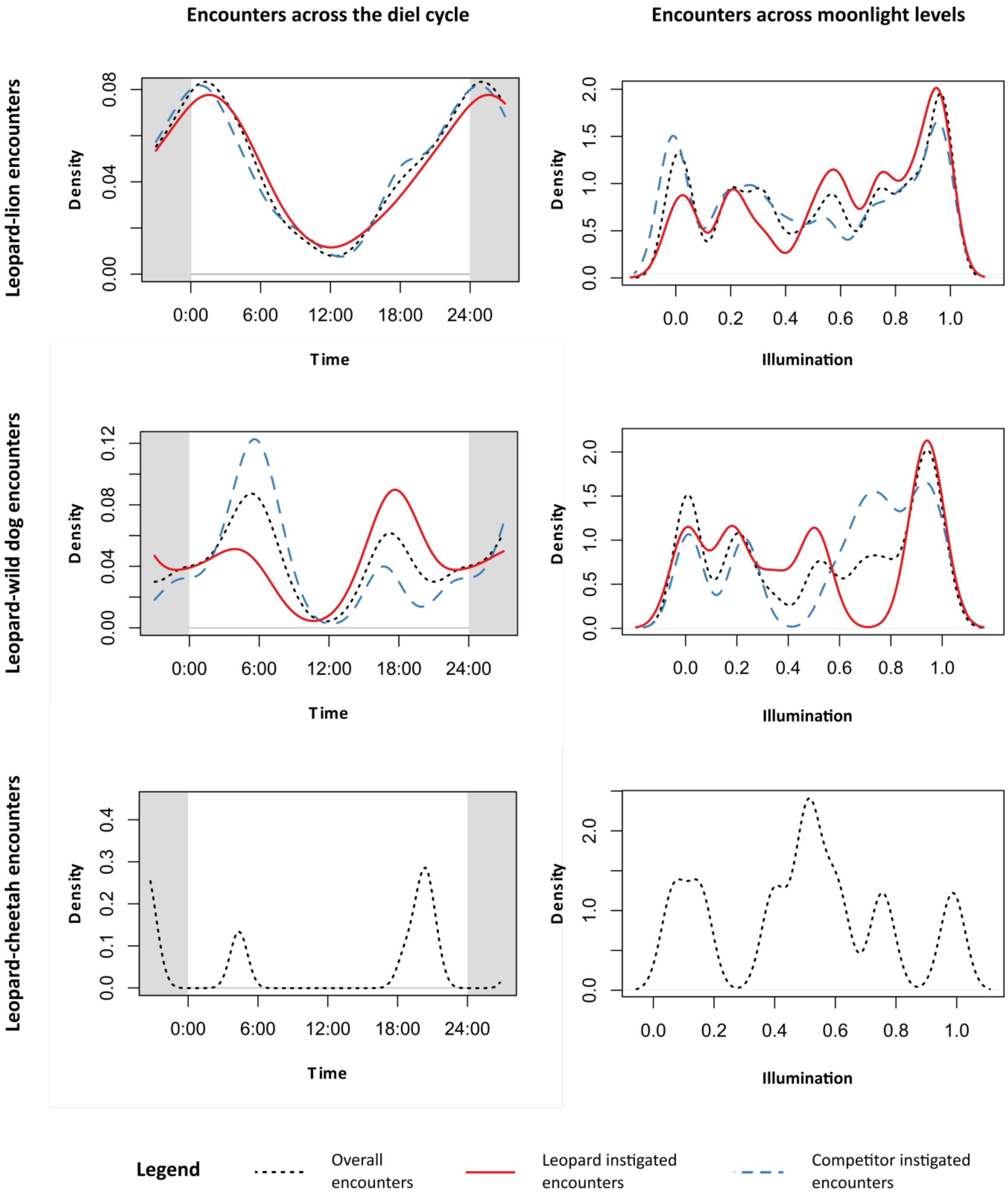

Figure 1: Leopard-competitor encounter peaks across diel cycles and moon illumination levels.

Encounter impacts on behaviour and movement

There was no significant difference in leopard first passage times when encountering lions (n = 64; 65.41 ± 1.77 minutes), wild dogs (n = 43; 68.00 ± 3.17), or cheetahs (n = 8; 113.70 ± 11.42), or in the first passage times of lions (n = 64; 47.58 ± 0.32), wild dogs (n = 43; 44.00 ± 0.305), and cheetahs (n = 8; 49.22 ± 1.11) when encountering leopards (Table S1-

S4). Habitat and species also had no impact on encounter durations (mean range: 36.60 ± 0.35 to 38.38 ± 1.15) (Tables S5-S6).

Whether leopards transitioned between stationary and movement activity states was not impacted by the species encountered (Fisher's exact, p = 0.309). Transitions were also unaffected by habitat type during leopard encounters with lions (Fisher's exact, p = 0.781), wild dogs (Fisher's exact, p = 1.000), and cheetahs (Fisher's exact, p = 1.000) (Table 3).

Table 3: Summary of leopard behavioural transitions between stationary (S) and movement (M) activity states in open and closed habitat types following encounters with lions, wild dogs, and cheetahs.

	Open habitat			Closed habitat			
Dyad	**M → S**	**S → M**	**No change**	**M → S**	**S → M**	**No change**	**Total**
Leopard-lion	1	3	7	8	9	36	64
Leopard-wild dog	1	0	4	9	4	25	43
Leopard-cheetah	0	0	2	0	2	4	8
Total	2	3	13	17	15	65	115

Leopard step lengths were larger following lion encounters, relative to controls, with the scale of this increase greatest following encounters within open habitats (Tables S7-S8; Figure 2a-b). Leopard step lengths did not change following wild dog encounters, and although there was a negative impact of cheetah encounters on leopard step lengths, compared to controls, the scale of this impact suggested little biological significance (Tables S7-S8; Figure 2a). Further, although for lion and wild dog encounters there was an impact of the treatment and time period terms on leopard tortuosity, changes were minimal, and biologically there seemed to be little significant difference (Table S9-S10;

Figure 2c-d). Leopard encounter site distances did not change in the 15 or 60 minute windows following encounters with any species (Table S11-S12).

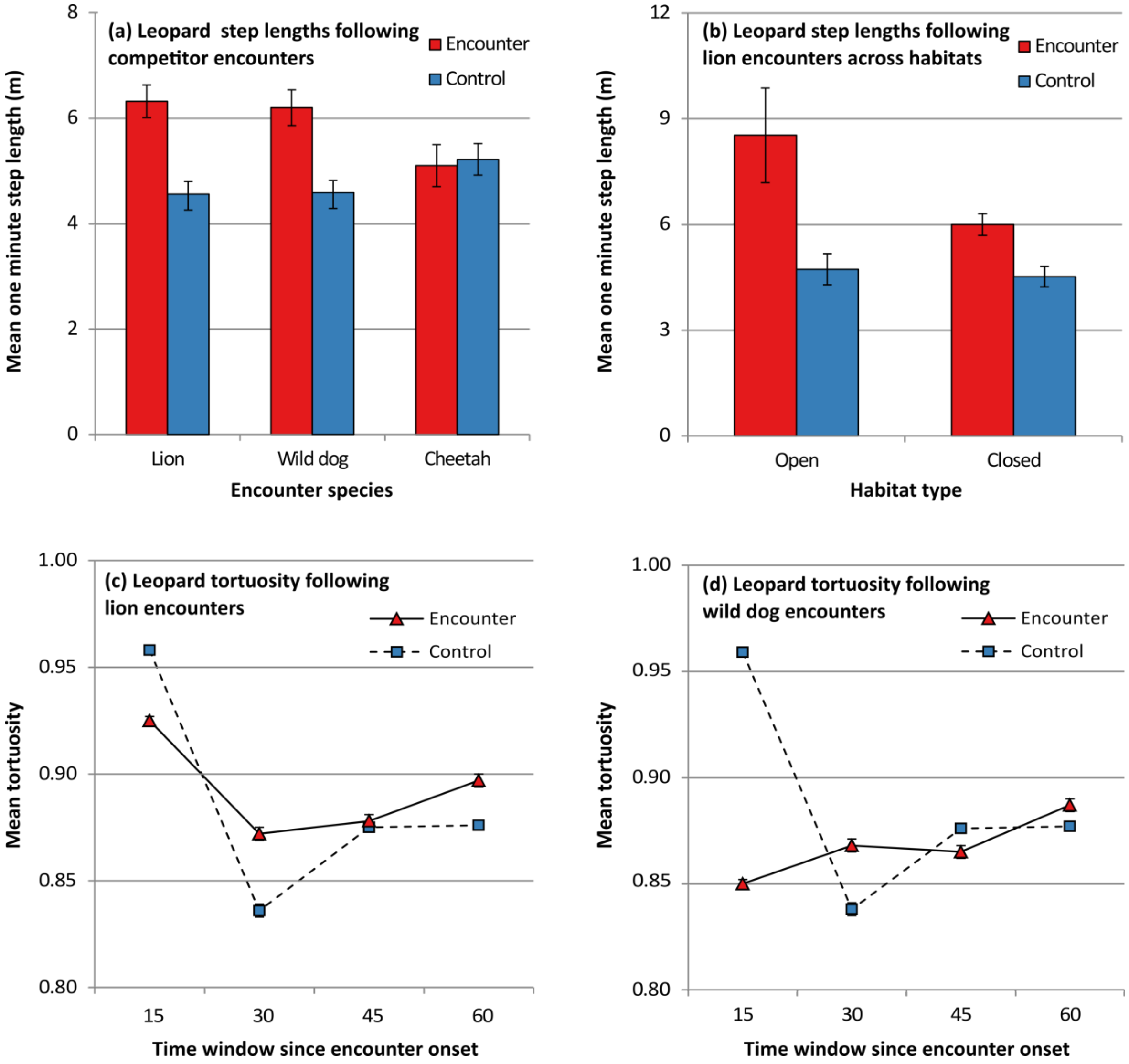

Figure 2: Post-encounter leopard movement metrics: (a) leopard mean one minute step lengths (m) across competitor species, (b) step lengths (m) following lion encounters within open and closed habitats, (c-d) path tortuosities following lion and wild dog encounters within consecutive 15 minute windows from encounter onsets.

Step lengths of lions, wild dogs, and cheetahs were larger following leopard than control encounters (Tables S13-S14; Figure 3a). For wild dogs, there was also an interaction between habitat and treatment. Specifically, steps lengths were three times larger following encounters within closed habitats, than controls, but they were 26 times larger following encounters within open habitats (Figure 3b). There was no significant impact of leopard encounters on lion, wild dog, or cheetah tortuosity (Tables S15-S16). However, lions and wild dogs did travel further from encounter sites, than from control sites, in the 15 and 60 minutes after encounters began (Tables S17-S18; Figure 3c-d). The scale of this increase was again larger for wild dogs in open than closed habitats (Figure 3e), but only within the 15 minute period following encounter onsets (Table S18). In contrast, for cheetahs, distances from encounter sites were no different between actual and control encounters (Table S18).

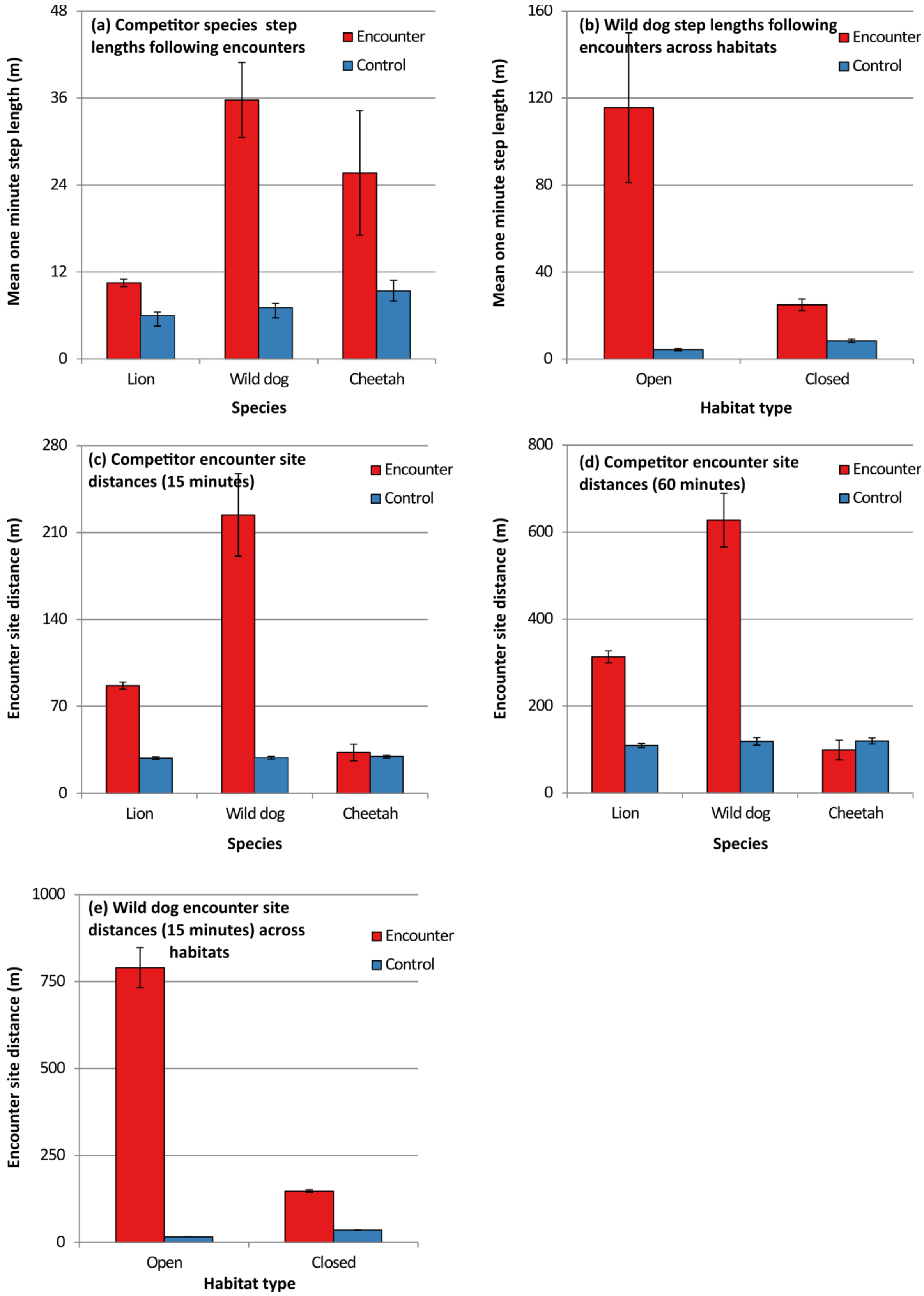

Figure 3: Post-encounter competitor movement metrics: (a) competitor mean one minute step lengths (m); (b) wild dog step lengths within open and closed habitats; (c-d) competitor encounter site distances

(m) 15 and 60 minutes after encounter onsets; (e) wild dog encounter site distances 15 minutes after encounters within open and closed habitats.

Movement in competitor presence

Mean leopard step lengths decreased when in close proximity to competitors, regardless of species (Table S19-S20; Figure 4). In contrast, there were no differences in step lengths for lions, wild dogs or cheetahs across different proximities to leopards (Table S21-S22).

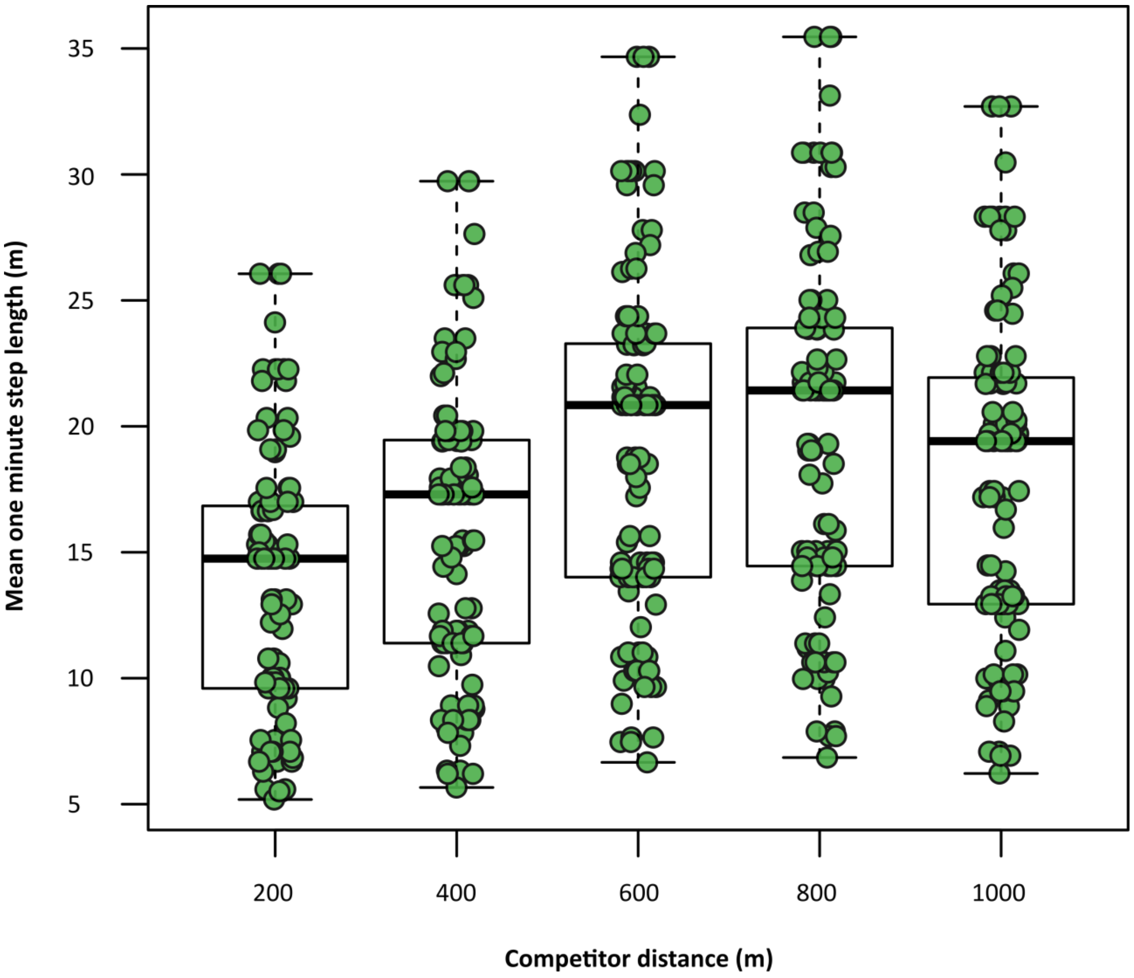

Figure 4: Mean leopard one minute step lengths (m) with increasing distance to competitors. Green points show raw predicted values.

Discussion

Our study showed that extensive overlap of activity patterns (see Cozzi et al 2012; Chapter 2) contributes to increased contacts between African predators but that leopard behaviours are only minimally impacted by encounters. Across the diel cycle, encounters with guild members peaked during periods of shared activity (Cozzi et al., 2012; Chapter 2), suggesting that activity overlaps increase competitor contact rates and that the cost of these overlaps are not fully offset by partitioning along other niche axes. This is important because animal activity patterns often show behavioural plasticity to fluctuating environments (Frey et al., 2017), and there is a growing body of evidence highlighting shifts in species niches caused by anthropogenic effects (Beckmann et al., 2012; Boivin et al., 2016; Creel et al., 2018; Kitchen et al., 2000). Our results suggest that within competitor assemblages, changes to species activity patterns that increase activity overlap could increase the strength of interference competition. For example, activity patterns are commonly thought to be driven by bottom-up forces (Kronfeld-Schor and Dayan, 2003), and so the simplification of prey resources (Creel et al., 2018) could conceivably lead to increased niche overlap across multiple axes (e.g. dietary, spatial, and temporal) within assemblages. Such shifts could lead to greater levels of top-down suppression of subordinate competitors, potentially inhibiting population growth and increasing a population’s susceptibility to localised extinctions through stochastic events (Carbone et al., 1997; Greenville et al., 2014). This is unlikely to be the case for leopards in Africa which, as we later suggest, appear relatively resilient to encounters with competitors; however, it is a concern for species that are particularly susceptible to the effects of interspecific competition e.g. African wild dogs (Carbone et al., 1997; Groom et al., 2017; Swanson et al., 2014).

Our results also show that encounters between African large predator guild members reflect imperfect decision making within heterogeneous environments, and to our knowledge our study is the first to look at encounters between large carnivores within this context. Leopards instigated encounters with (likely) dominant competitors (e.g. lions and wild dogs) within closed habitats as often as competitors did, but they rarely instigated encounters within open habitats. This suggests that: (1) leopards are competitively inferior to lions and wild dogs and tend to avoid encounters in open habitats; (2) habitats with reduced visibility limit the leopard's ability to accurately assess immediate competitor risk; and (3) habitat structure plays a role in mediating encounter occurrences between competitors (Janssen et al., 2007).

In open habitats, long-range detection of competitors may have allowed leopards to adapt movement directions to maintain spatial distances over the encounter threshold, whilst in closed habitats, detection may have been limited to short-distances. Interestingly, Vanak et al. (2013) found that leopards avoided areas recently occupied by lions during the dry season but not during the wet season, and this may, perhaps, reflect the difficulties in assessing competitor risk during seasons with increased vegetation cover. Our leopard instigated encounters may thus have been a consequence of leopards approaching areas of interest (e.g. potential carcasses) without being aware of competitor presence or of opportunistic encounters arising from inadvertently occupying the same areas in close proximity to competitors. As such, similar as for prey detection, visual cues appear to be the primary sensory mechanism used in immediate risk assessment, whilst olfactory and auditory information appears to play a limited role, perhaps because such signals are not always available (Sunquist and Sunquist, 2002). Olfactory cues, for example, require suitable environmental conditions (e.g. wind direction) for detection, and the information they provide can depend on a range of factors, including location and time since deposition (Parsons et al., 2018). Higher numbers of leopard instigated encounters within closed habitats could also have occurred if leopards were aware of lion presence but still chose to approach due to a shared resource or curiosity and the ability to move quickly to a safe tree if attacked (Bailey, 2005). Whilst closed habitats can provide vertical refuge for leopards, considering the increased ambush risks associated with these areas and mortality risks associated with encountering lions (Bailey, 2005; Hopcraft et al., 2005), we find the chance that they approach with intent unlikely. Instead, higher numbers of encounters within closed habitats likely reflect (1) the shared occupancy of these areas, perhaps occurring as a result of similar resource acquisition strategies, and (2) the difficulties of detecting competitors within these areas.

Excluding cheetah encounters, for which we had a limited sample size, encounters peaked for all dyads during periods of high moonlight illumination. Given that not all guild species' activity levels are influenced by moonlight availability (Cozzi et al., 2012; Chapter 2), this may reflect the lower risks associated with approaching potentially contested resources during periods of high illumination, e.g. reduced lion ambush risks because of greater visibility (Funston et al., 2001; Packer et al., 2011). Alternatively, encounter peaks across moonlight levels may have been driven by periodicity in the use of shared areas of home ranges, which in turn, may have been driven by periodicity in resource distributions (Jarman and Jarman, 1973; Riotte-Lambert et al., 2013). For example, impala (*Aepyceros melampus*), a favoured prey species of leopards (Hayward et al., 2006), can show periodicity in the use of some open habitats within their home range, with use declining during full moon periods (Riotte-Lambert et al., 2013). If similar patterns of periodicity drive the space use of other prey species and/or cause prey to congregate into similar habitat patches, e.g. to reduce predation risk through mixed herd benefits (Kiffner et al., 2014; Schmitt et al., 2016), then increased encounters during high moonlight illumination may reflect the attraction of competitors to habitat patches with high periodic resource availability. Interestingly, some encounters also peaked during periods of low light availability. This may simply reflect the impacts of low light levels on species detectability (Funston et al., 2001; Packer et al., 2011). In other words, encounters may have increased during these periods because species were able to travel closer to other guild members, with or without intent, without being detected. However, that leopard instigated lion encounters also did not show a peak during low moonlight periods suggests that leopards were still able to detect and avoid instigating lion encounters and suggests that the other species' peaks in encounters may have been species approaching guild members with purpose.

That encounters did not cause leopards to change behavioural states suggests that competitors have a minimal impact on leopard behaviour (Maputla et al., 2015; Miller et al., 2018). This also suggests that when resting and being approached by competitors, leopards are either within concealed areas where the risk of detection is low and/or in trees where the chances of injury are negligible. It is likely that during some encounters leopards did seek refuge in trees upon detecting competitors. However, activity states and first passage times were unaffected by encounters across guild species, suggesting that although tree occupancy may have been driven by competitor avoidance, the costs of such avoidance behaviours were low, e.g. since long-term behavioural states remained unaffected. As such, our results support the hypothesis that leopards are largely able to withstand the effects of intraguild competition and that this is facilitated by aspects of their ecology and life history that reduce detection probabilities and encounter costs (Bailey, 2005; Balme et al., 2017a; Miller et al., 2018). When resting within largely open areas where the risk of detection is high, for example, leopards can mitigate the costs of encounters by exploiting micro-scale competition refuges (i.e. trees) unavailable to other guild species (Bailey, 2005).

Having said this, the energetic costs of encounters remain unknown. For example, the loss of kills remained cryptic to our sampling regime, and whilst prey caching does reduce kleptoparasitism, leopard reproductive success is still affected by kill loss (Balme et al., 2017a). Large carnivores are thought to be energetically constrained due to the energetic requirements imposed by larger body masses and the hunting costs associated with taking larger prey species, and so the loss of kills to competitors could make leopards energetically vulnerable (Balme et al., 2017a; Carbone et al., 2007). Work to remotely detect kill sites from our radio collar accelerometer and GPS data is currently ongoing, and an in-depth analysis of the energetic costs of prey capture, kleptoparasitism, and hoisting behaviour is expected to form the basis of a future study.

Our results that leopards increased step lengths upon encountering lions and that the scale of this increase was greatest within open habitats are consistent with other studies: leopards increase step lengths when already moving in order to gain distance from competitors, with the scale of the change reflecting the risks associated with different habitats (Du Preez et al., 2015). Thus, larger step lengths following encounters within open habitats may reflect the lack of vertical refuges and/or the inability to use crypsis as an escape/avoidance tactic.

Interestingly, we found that leopards reduced step lengths when in close proximity to competitors, irrespective of competitor species, with step lengths increasing as competitor proximity decreased. These reductions in leopard step lengths may have reflected slower, cautious periods of travel through areas with a perceived higher competitor risk, rather than an omniscient knowledge of competitor presence and distance, which as we have discussed earlier is unlikely to exist. Thus, our results suggest that leopard movements may be impacted by competitors at two scales, i.e. *via* both direct and indirect cues of competitor presence and risk. Such patterns could occur if, for example, competitors select for habitat patches with similar resource availability, within which periods of close proximity to competitors most commonly occur (Rich et al., 2017). Of course, in this case, leopard step lengths may also have been conflated with resource acquisition strategies; in other words, leopards may move slower or engage in more stalking behaviours when moving through prey rich areas to increase hunting success (Bailey, 2005). We were unable to explore these two hypotheses further because habitat maps of our study area were unavailable within this project's timeframe. Future studies would benefit from including habitat features into models in order to tease apart the impacts of bottom-up and top-down forces on leopard movement parameters.

Following leopard encounters, step lengths increased for lions, wild dogs and cheetahs. Although we find it difficult to ascribe function to these changes without knowledge of the potential contested resources at encounter sites, we can speculate that the underlying drivers of these changes differed between species. For example, increases in step length and path linearity have been associated with the movements of large carnivores through high risk areas (Oriol-Cotterill et al., 2015), and so for cheetahs, increased step lengths may reflect injury risks posed by leopards (Bailey, 2005). However, we find the results that wild dog step lengths and encounter site distances were larger following leopard encounters within open than closed habitats unusual, because these are the habitats where mobbing of leopards by wild dogs is conceivably easier for wild dog packs (e.g. Downer, 2017). Further, given the mortality, injury, and kleptoparasitism risks posed to leopards by lions, we find it unlikely that lions were fleeing from leopard encounters. Yet, anecdotal evidence from lion and wild dog encounter animations suggest that these species were not chasing after leopards. Thus, considered alongside the species' relative competitive mass to leopards, we find these results difficult to explain. Ultimately, it is likely that changes in movement parameters following encounters reflect individual species life histories and the circumstances under which encounters take place.

In summary, our results show that encounters between competitors are (1) influenced by factors which contribute to imperfect decision making and/or which increase niche axes overlaps, and (2) highlight the extent that the costs of encounters may be mitigated by a species' life history traits and ecology. We found that leopards, despite high levels of temporal activity overlap with competitors and accompanying increases in encounters within overlap periods, are able to coexist alongside other large African predators with minimal behavioural and movement costs. Whilst further work is needed on the energetic consequences of encounters, our results show that considering the factors driving competitor contacts and considering the costs of encounters can provide insights into how human-mediated shifts along niche axes (e.g. Creel et al., 2018; Kitchen et al., 2000) may impact intraguild competition dynamics.

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Author contributions

KR, NJ, and KG conceived the study; KR collected the majority of the leopard data (with other data provided by the BPCT), carried out the analyses, and wrote the manuscript; NJ, CM, MH, and KG contributed to manuscript revisions. AW provided radio collars for the project. JM provided the research infrastructure for field data collection.

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Supplementary Materials

Figure S1: Example of the type of histogram, i.e. showing the frequency of leopard one minute step lengths, used to choose the < 1 m step length threshold for defining stationary (red) and movement (green) behaviours.

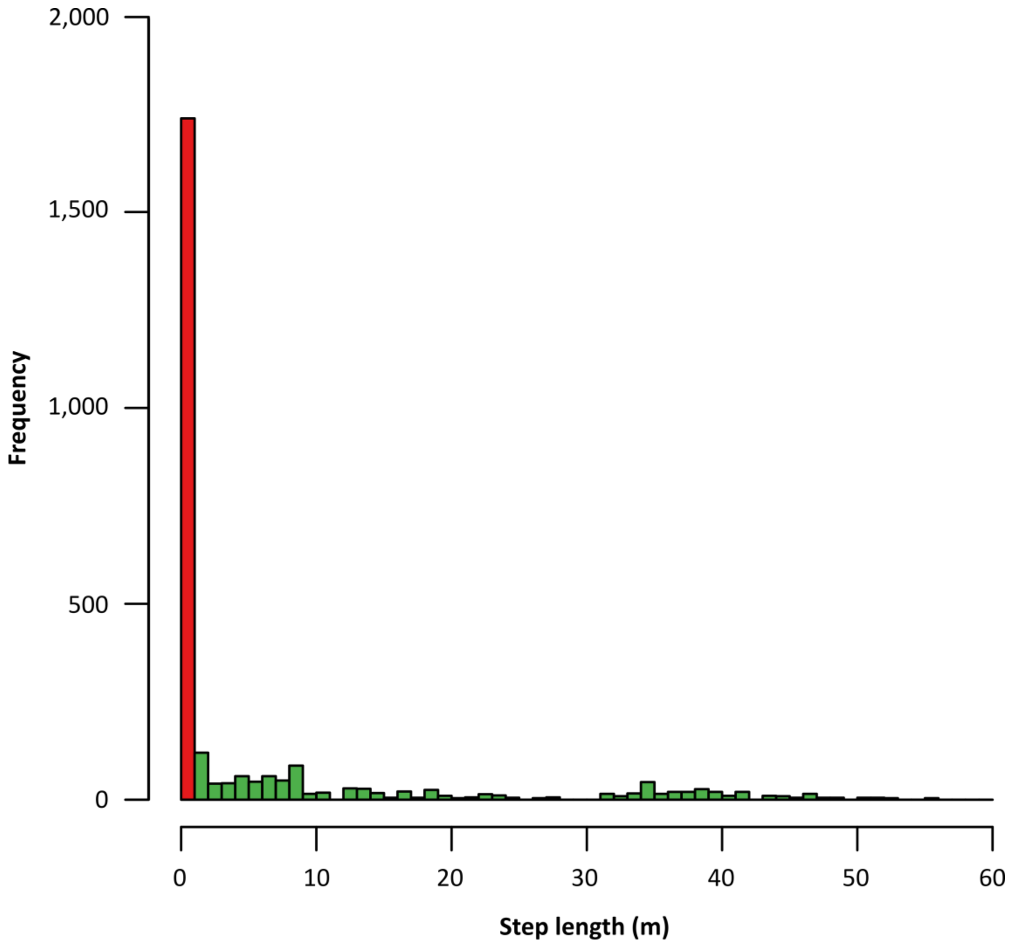

Table S1: Summary of candidate models (Δ AIC$_C$ < 6) of linear mixed-effects modelling output investigating leopard first passage times following competitor encounters.

Model	**R^2**	**K**	**AIC$_c$**	**Δ AIC$_c$**	**Wi**
Null model	0.015	4	366.432	-	0.436
Species	0.045	6	367.483	1.050	0.258
Habitat	0.020	5	368.074	1.641	0.192
Species + habitat	0.050	7	369.102	2.670	0.115

K = degrees of freedom; AIC$_C$ = Akaike's Information Criterion corrected for small sample sizes; Δ AIC$_c$ = difference between this models AIC$_C$ with the lowest AIC$_C$ value out of all models; Wi = Akaike weight. Random effects variable variances (± SD): leopard ID, 0.307 ± 0.001; competitor ID, 0.930 ± 0.305.

Table S2: Model averaged parameter estimates derived from linear mixed-effects candidate models (Table S1) investigating leopard first passage times following competitor encounters.

				Confidence Interval	
Parameter	**Estimate**	**SE**	**Adj. SE**	**Lower**	**Upper**
(Intercept)	4.606	0.513	0.515	3.596	5.616
Species (wild dog)	-0.280	0.478	0.480	-1.759	0.254
Species (lion)	-0.348	0.543	0.544	-1.911	0.044
Habitat (open)	-0.073	0.200	0.202	-0.838	0.363

Table S3: Summary of candidate models (Δ AIC_C < 6) of linear mixed-effects modelling output investigating competitor first passage times following leopard encounters.

Model	**R^2**	**K**	**AIC_c**	**Δ AIC_c**	**Wi**
Null	0.000	4	372.267	-	0.464
Habitat	0.012	5	373.094	0.827	0.307
Species	0.019	6	374.553	2.286	0.148
Species + habitat	0.029	7	375.730	3.463	0.082

K = degrees of freedom; AIC_C = Akaike's Information Criterion corrected for small sample sizes; Δ AIC_c = difference between this models AIC_C with the lowest AIC_C value out of all models; Wi = Akaike weight. Random effects variable variances (± SD): leopard ID, 0.001 ± 0.001 competitor ID, 0.001 ± 0.001.

Table S4: Model averaged parameter estimates derived from linear mixed-effects candidate models (Table S3) investigating competitor first passage times following leopard encounters.

				Confidence Interval	
Parameter	**Estimate**	**SE**	**Adj. SE**	**Lower**	**Upper**
(Intercept)	3.861	0.244	0.000	3.378	4.344
Habitat (open)	0.133	0.253	0.600	-0.259	0.945
Species (wild dog)	-0.094	0.278	0.738	-1.312	0.497
Species (lion)	-0.023	0.217	0.916	-0.980	0.778

Table S5: Summary of candidate models (Δ AIC_C < 6) of linear mixed-effects modelling output investigating encounter durations.

Model	R^2	K	AIC_c	Δ AIC_c	Wi
Habitat	0.032	5.000	1032.954	-	0.597
Null	0.000	4.000	1034.525	1.571	0.272
Species + habitat	0.037	7.000	1036.921	3.967	0.082
Species	0.008	6.000	1037.968	5.014	0.049

K = degrees of freedom; AIC_C = Akaike's Information Criterion corrected for small sample sizes; Δ AIC_c = difference between this models AIC_C with the lowest AIC_C value out of all models; Wi = Akaike weight. Random effects variable variances (± SD): leopard ID, 4.383 ± 2.094; competitor ID, 4.765 ± 2.183.

Table S6: Model averaged parameter estimates derived from linear mixed-effects candidate models (Table S5) investigating encounter durations.

				Confidence Interval	
Parameter	**Estimate**	**SE**	**Adj. SE**	**Lower**	**Upper**
(Intercept)	36.614	4.082	4.113	28.552	44.676
Habitat (open)	7.034	6.543	6.576	-0.246	20.959
Species (wild dog)	-0.819	3.663	3.691	-22.669	10.152
Species (lion)	-0.990	3.866	3.891	-23.488	8.352

Table S7: Summary of candidate models (Δ AIC_C < 6) of linear mixed-effects modelling output investigating leopard step length following competitor encounters. Within the model column, models are grouped by which dyad they represent (bold).

Model	R^2	K	AIC_c	Δ AIC_c	Wi
Leopard-lion					
Treatment + habitat + treatment x habitat	0.173	8	2550.896	-	0.855
Treatment	0.161	6	2554.461	3.565	0.144
Leopard-wild dog					
Treatment	0.188	6	2127.940	-	0.482
Null	0.182	5	2128.500	0.559	0.364
Treatment + habitat + treatment x habitat	0.192	8	2130.244	2.304	0.152
Leopard-cheetah					
Treatment	0.227	6	1640.963	-	0.908
Null	0.214	5	1645.752	4.789	0.083

K = degrees of freedom; AIC_C = Akaike's Information Criterion corrected for small sample sizes; Δ AIC_c = difference between this models AIC_C with the lowest AIC_C value out of all models; Wi = Akaike weight. Random effects variable variances can be found in Table S23.

Table S8: Model averaged parameter estimates derived from linear mixed-effects candidate models (Table S7) investigating leopard step length following competitor encounters. Within the parameter column, parameters are grouped by which dyad they represent (bold). * denotes model parameters that had a significant impact on leopard step lengths.

				Confidence Interval	
Parameter	**Estimate**	**SE**	**Adj. SE**	**Lower**	**Upper**
Leopard-lion					
(Intercept)	1.144	0.278	0.279	0.598	1.690
Treatment (encounter) *	0.579	0.185	0.185	0.216	0.943
Habitat (open)	0.023	0.188	0.188	-0.372	0.425
Habitat (open) x treatment (encounter) *	0.811	0.469	0.469	0.246	1.648
Leopard-wild dog					
(Intercept)	1.001	0.386	0.387	0.242	1.759
Treatment (encounter)	0.214	0.219	0.219	-0.025	0.698
Habitat (open)	-0.010	0.081	0.081	-0.455	0.319
Habitat (open) x treatment (encounter)	0.143	0.407	0.407	-0.218	2.088
Leopard-cheetah					
(Intercept)	1.167	0.329	0.330	0.521	1.814
Treatment (encounter) *	-1.090	0.549	0.550	-2.093	-0.287

Table S9: Summary of candidate models (Δ AIC$_C$ < 6) of linear mixed-effects modelling output investigating leopard path tortuosity following competitor encounters. Within the model column, models are grouped by which dyad they represent (bold).

Model	**R^2**	**K**	**AIC$_c$**	**Δ AIC$_c$**	**Wi**
Leopard-lion					
Treatment + time + treatment x time	0.070	12	2177.892	-	0.953
Leopard-wild dog					
Treatment + time + treatment x time	0.063	12	1939.633	-	0.878
Treatment + time + habitat + treatment x time + treatment x habitat	0.065	14	1943.648	4.015	0.118
Leopard-cheetah					
Null	-0.067	5	-40.929	-	0.919
Treatment	0.054	6	-36.074	4.854	0.081

K = degrees of freedom; AIC$_C$ = Akaike's Information Criterion corrected for small sample sizes; Δ AIC$_c$ = difference between this models AIC$_C$ with the lowest AIC$_C$ value out of all models; Wi = Akaike weight. Random effects variable variances can be found in Table S23.

Table S10: Model averaged parameter estimates derived from linear mixed-effects candidate models (Table S9) investigating leopard path tortuosity following competitor encounters. Within the parameter column, parameters are grouped by which dyad they represent (bold). * denotes model parameters that had a significant impact on leopard path tortuosity.

				Confidence Interval	
Parameter	**Estimate**	**SE**	**Adj. SE**	**Lower**	**Upper**
Leopard-lion					
(Intercept)	3.082	0.235	-	2.633	3.530
Treatment (experiment) *	-0.688	0.319	-	-1.298	-0.040
Time (30) *	-1.501	0.269	-	-2.021	-0.970
Time (45) *	-1.187	0.269	-	-1.707	-0.656
Time (60) *	-1.181	0.269	-	-1.701	-0.651
Treatment (experiment) x time (30) *	0.890	0.407	-	0.090	1.680
Treatment (experiment) x time (45)	0.639	0.409	-	-0.163	1.432
Treatment (experiment) x time (60) *	0.819	0.409	-	0.175	1.613
Leopard-wild dog					
(Intercept)	3.125	0.228	0.229	2.677	3.573
Treatment (experiment) *	-1.384	0.362	0.363	-2.096	-0.672
Time (30) *	-1.508	0.282	0.282	-2.061	-0.955
Time (45) *	-1.192	0.281	0.282	-1.745	-0.639
Time (60) *	-1.186	0.281	0.282	-1.739	-0.633
Treatment (experiment) x time (30) *	1.653	0.474	0.475	0.721	2.585
Treatment (experiment) x time (45) *	1.311	0.474	0.475	0.379	2.243
Treatment (experiment) x time (60) *	1.507	0.474	0.475	0.575	2.438
Habitat (open)	-0.009	0.073	0.073	-0.469	0.310
Treatment (experiment) x habitat (open)	0.076	0.271	0.272	-0.356	1.641
Leopard-cheetah					
(Intercept)	0.812	0.018	0.018	0.777	0.847
Treatment (experiment)	-0.005	0.021	0.021	-0.156	0.039

Table S11: Summary of candidate models (Δ AIC_C < 6) of linear mixed-effects modelling output investigating leopard distances from encounter sites following competitor encounters. Within the model column, models are grouped by which dyad and post-encounter time period they represent (bold).

Model	R^2	K	AIC_c	Δ AIC_c	Wi
Leopard-lion (15 minutes post-encounter)					
Treatment	0.163	6	705.092	-	0.468
Null	-0.110	5	705.668	0.577	0.351
Treatment + habitat + treatment x habitat	0.022	8	706.984	1.892	0.182
Leopard-lion (60 minutes post-encounter)					
Null	0.001	5	701.625	-	0.655
Treatment	0.003	6	703.373	1.748	0.273
Treatment + habitat + treatment x habitat	0.005	8	706.059	4.434	0.071
Leopard-wild dog (15 minutes post-encounter)					
Null	0.006	5	594.774	-	0.659
Treatment	0.010	6	596.708	1.934	0.251
Treatment + habitat + treatment x habitat	0.012	8	598.749	3.975	0.090
Leopard-wild dog (60 minutes post-encounter)					
Null	0.000	5	585.797	-	0.413
Treatment	0.016	6	585.923	0.126	0.388
Treatment + habitat + treatment x habitat	0.025	8	587.259	1.462	0.199
Leopard-cheetah (15 minutes post-encounter)					
Null	0.000	5	831.393	-	0.631
Treatment	0.011	6	832.465	1.071	0.369
Leopard-cheetah (60 minutes post-encounter)					
Null	0.016	5	711.385	-	0.750
Treatment	0.016	6	713.580	2.194	0.250

K = degrees of freedom; AIC_C = Akaike's Information Criterion corrected for small sample sizes; Δ AIC_c = difference between this models AIC_C with the lowest AIC_C value out of all models; Wi = Akaike weight. Random effects variable variances can be found in Table S23.

Table S12: Model averaged parameter estimates derived from linear mixed-effects candidate models (Table S11) investigating leopard distances from encounter sites following competitor encounters. Within the parameter column, parameters are grouped by which dyad and post-encounter time period they represent (bold).

				Confidence Interval	
Parameter	**Estimate**	**SE**	**Adj. SE**	**Lower**	**Upper**
Leopard-lion (15 minutes post-encounter)					
(Intercept)	3.415	0.299	0.302	2.823	4.006
Treatment (encounter)	0.384	0.422	0.424	-0.178	1.360
Habitat (open)	-0.020	0.201	0.203	-1.021	0.801
Treatment (encounter) x habitat (open)	0.155	0.490	0.492	-0.830	2.535
Leopard-lion (60 minutes post-encounter)					
(Intercept)	4.980	0.230	0.232	4.526	5.434
Treatment (encounter)	0.102	0.259	0.261	-0.436	1.029
Habitat (open)	0.006	0.125	0.126	-0.824	0.994
Treatment (encounter) x habitat (open)	0.020	0.237	0.239	-1.403	1.950
Leopard-wild dog (15 minutes post-encounter)					
(Intercept)	3.167	0.360	0.364	2.454	3.879
Treatment (encounter)	0.066	0.256	0.258	-0.614	1.003
Habitat (open)	-0.008	0.134	0.136	-0.955	0.785
Treatment (encounter) x habitat (open)	0.055	0.396	0.399	-1.731	2.947
Leopard-wild dog (60 minutes post-encounter)					
(Intercept)	4.967	0.224	0.226	4.524	5.409
Treatment (encounter)	0.306	0.396	0.398	-0.258	1.299
Habitat (open)	0.011	0.191	0.193	-0.789	0.896
Treatment (encounter) x habitat (open)	0.204	0.627	0.630	-1.086	3.133
Leopard-cheetah (15 minutes post-encounter)					
(Intercept)	17.627	1.428	1.445	14.794	20.461
Treatment (encounter)	-2.286	4.288	4.317	-16.242	3.853
Leopard-cheetah (60 minutes post-encounter)					
(Intercept)	8.990	0.890	0.901	7.224	10.755
Treatment (encounter)	-0.252	1.527	0.870	-6.814	4.800

Table S13: Summary of candidate models (Δ AIC_C < 6) of linear mixed-effects modelling output investigating competitor step length following leopard encounters. Within the model column, models are grouped by which dyad they represent (bold).

Model	R^2	K	AIC_c	Δ AIC_c	Wi
Leopard-lion					
Treatment + habitat + habitat x treatment	0.203	8	2668.714	-	0.745
Treatment	0.193	6	2670.858	2.144	0.255
Leopard-wild dog					
Treatment + habitat + habitat + treatment	0.306	8	2306.718	-	0.999
Leopard-cheetah					
Treatment	0.265	6	1790.193	-	0.993

K = degrees of freedom; AIC_C = Akaike's Information Criterion corrected for small sample sizes; Δ AIC_c = difference between this models AIC_C with the lowest AIC_C value out of all models; Wi = Akaike weight. Random effects variable variances can be found in Table S24.

Table S14: Model averaged parameter estimates derived from linear mixed-effects candidate models (Table S13) investigating competitor step length following leopard encounters. Within the parameter column, parameters are grouped by which dyad they represent (bold). * denotes model parameters that had a significant impact on competitor step lengths.

				Confidence Interval	
Parameter	**Estimate**	**SE**	**Adj. SE**	**Lower**	**Upper**
Leopard-lion					
(Intercept)	1.144	0.341	0.342	0.475	1.813
Treatment (encounter) *	0.913	0.216	0.216	0.489	1.337
Habitat (open) *	-0.479	0.343	0.343	-1.092	-0.193
Habitat (open) x treatment (encounter)	0.349	0.400	0.400	-0.314	1.250
Leopard-wild dog					
(Intercept)	1.230	0.297	-	0.537	1.413
Treatment (encounter) *	1.046	0.225	-	0.605	1.487
Habitat (open) *	-0.726	0.232	-	-1.180	-0.271
Habitat (open) x treatment (encounter) *	3.159	0.695	-	1.797	4.517
Leopard-cheetah					
(Intercept)	0.191	0.514	-	-0.929	1.259
Treatment (encounter) *	2.667	0.462	-	1.730	3.566

Table S15: Summary of candidate models (Δ AIC$_C$ < 6) of linear mixed-effects modelling output investigating competitor path tortuosity following leopard encounters. Within the model column, models are grouped by which dyad they represent (bold).

Model	R^2	K	AIC$_c$	Δ AIC$_c$	Wi
Leopard-lion					
Treatment + time + treatment x time	0.116	12	2422.520	-	0.814
Treatment + time + habitat + treatment x time + treatment x habitat	0.120	14	2425.470	2.949	0.186
Leopard-wild dog					
Treatment + time + treatment x time	0.852	12	2043.966	-	0.752
Treatment + time + habitat + treatment x time + treatment x habitat	0.090	14	2046.195	2.229	0.247
Leopard-cheetah					
Treatment + time + treatment x time	0.096	12	1506.023	-	0.976

K = degrees of freedom; AIC$_C$ = Akaike's Information Criterion corrected for small sample sizes; Δ AIC$_c$ = difference between this models AIC$_C$ with the lowest AIC$_C$ value out of all models; Wi = Akaike weight. Random effects variable variances can be found in Table S24.

Table S16: Model averaged parameter estimates derived from linear mixed-effects candidate models (Table S15) investigating competitor path tortuosity following leopard encounters. Within the parameter column, parameters are grouped by which dyad they represent (bold). * denotes model parameters that had a significant impact on competitor path tortuosity.

Parameter	Estimate	SE	Adj. SE	Lower	Upper
Leopard-lion					
(Intercept)	2.557	0.350	0.350	1.870	3.243
Treatment (experiment)	0.126	0.344	0.345	-0.550	0.801
Time (30) *	-1.049	0.289	0.289	-1.616	-0.482
Time (45) *	-1.112	0.289	0.289	-1.679	-0.546
Time (60) *	-0.888	0.289	0.289	-1.455	-0.321
Treatment (experiment) x time (30)	-0.099	0.435	0.436	-0.954	0.756
Treatment (experiment) x time (45)	-0.022	0.435	0.436	-0.877	0.833
Treatment (experiment) x time (60)	-0.553	0.437	0.438	-1.412	0.306
Habitat (open)	0.060	0.155	0.155	-0.103	0.742
Treatment (experiment) x habitat (open)	-0.102	0.272	0.272	-1.315	0.217
Leopard-wild dog					
(Intercept)	2.708	0.303	0.304	2.113	3.304
Treatment (experiment)	-0.081	0.373	0.374	-0.814	0.651
Time (30)*	-1.064	0.280	0.281	-1.615	-0.514
Time (45) *	-1.128	0.280	0.281	-1.678	-0.577
Time (60) *	-0.903	0.280	0.281	-1.454	-0.353
Treatment (experiment) x time (30)	-0.432	0.477	0.478	-1.370	0.505
Treatment (experiment) x time (45)	0.153	0.479	0.480	-0.788	1.095
Treatment (experiment) x time (60)	0.212	0.479	0.480	-0.730	1.153
Habitat (open)	0.083	0.178	0.179	-0.077	0.748
Treatment (experiment) x habitat (open)	-0.146	0.383	0.383	-1.719	0.538
Leopard-cheetah					
(Intercept)	2.671	0.301	-	2.065	3.225
Treatment (experiment)	0.088	0.788	-	-1.404	1.689
Time (30) *	-1.080	0.277	-	-1.623	-0.539
Time (45) *	-1.148	0.278	-	-1.691	-0.605
Time (60) *	-0.929	0.278	-	-1.471	-0.385
Treatment (experiment) x time (30)	0.294	0.960	-	-1.602	2.149
Treatment (experiment) x time (45)	0.145	0.961	-	-1.752	1.999
Treatment (experiment) x time (60)	0.185	0.961	-	-1.712	2.039

Table S17: Summary of candidate models (Δ AIC_C < 6) of linear mixed-effects modelling output investigating competitor encounter site distances following leopard encounters. Within the model column, models are grouped by which dyad and post-encounter time period they represent (bold).

Model	R^2	K	AIC_c	Δ AIC_c	Wi
Leopard-lion (15 minutes post-encounter)					
Treatment + habitat + treatment x habitat	0.082	8	723.546	-	0.642
Treatment	0.057	6	724.786	1.239	0.345
Null	0.003	5	731.303	7.756	0.013
Leopard-lion (60 minutes post-encounter)					
Treatment	0.071	6	715.784	-	0.596
Treatment + habitat + treatment x habitat	0.083	8	716.792	1.008	0.360
Null	0.026	5	720.969	5.184	0.045
Leopard-wild dog (15 minutes post-encounter)					
Treatment + habitat + treatment x habitat	0.154	8	631.952	-	0.877
Treatment	0.117	6	635.882	3.930	0.123
Null	0.008	5	648.640	16.688	0.000
Leopard-wild dog (60 minutes post-encounter)					
Treatment + habitat + treatment x habitat	0.152	8	611.067	-	0.696
Treatment	0.127	6	612.729	1.663	0.303
Null	0.033	5	624.149	13.083	0.001
Leopard-cheetah (15 minutes post-encounter)					
Null	-0.001	5	120.791	-	0.937
Treatment	0.145	6	126.175	5.384	0.063
Leopard-cheetah: (60 minute post-encounter)					
Null	-0.007	5	134.506	-	0.927
Treatment	0.160	6	139.578	5.072	0.073

K = degrees of freedom; AIC_C = Akaike's Information Criterion corrected for small sample sizes; Δ AIC_c = difference between this models AIC_C with the lowest AIC_C value out of all models; Wi = Akaike weight. Random effects variable variances can be found in Table S24.

Table S18: Model averaged parameter estimates derived from linear mixed-effects candidate models (Table S17) investigating competitor encounter site distances following leopard encounters. Within the parameter column, parameters are grouped by which dyad and post-encounter time period they represent (bold). * denotes model parameters that had a significant impact on competitor distances.

				Confidence Interval	
Parameter	**Estimate**	**SE**	**Adj. SE**	**Lower**	**Upper**
Leopard-lion (15 minutes post-encounter)					
(Intercept)	3.518	0.378	0.380	2.772	4.264
Treatment (encounter) *	1.061	0.434	0.438	0.203	1.919
Habitat (open)	-0.574	0.583	0.585	-1.869	0.103
Treatment (encounter) x habitat (open)	0.081	0.744	0.750	-1.693	1.940
Leopard-lion (60 minutes post-encounter)					
(Intercept)	4.546	0.384	0.387	3.787	5.304
Treatment (encounter) *	0.983	0.458	0.461	0.207	1.850
Habitat (open)	-0.230	0.424	0.425	-1.602	0.325
Treatment (encounter) x habitat (open)	0.102	0.554	0.558	-1.484	2.053
Leopard-wild dog (15 minutes post-encounter)					
(Intercept)	3.587	0.336	0.339	2.923	4.252
Treatment (encounter) *	1.399	0.539	0.543	0.334	2.463
Habitat (open)	-0.786	0.567	0.571	-1.921	0.129
Treatment (encounter) x habitat (open) *	2.547	1.551	1.561	0.318	5.490
Leopard-wild dog (60 minutes post-encounter)					
(Intercept)	4.569	0.447	0.451	3.684	5.454
Treatment (encounter) *	1.440	0.506	0.511	0.439	2.441
Habitat (open)	-0.350	0.460	0.464	-1.446	0.440
Treatment (encounter) x habitat (open)	1.695	1.523	1.529	-0.017	4.883
Leopard-cheetah (15 minutes post-encounter)					
(Intercept)	13.237	6.575	7.584	-1.626	28.101
Treatment (encounter)	0.717	3.176	3.350	-3.557	26.146
Leopard-cheetah (60 minute post-encounter)					
(Intercept)	23.317	11.960	13.778	-3.687	50.322
Treatment (encounter)	1.432	5.825	6.131	-5.222	44.263

Table S19: Summary of candidate models (Δ AIC_C < 6) of linear mixed-effects modelling output investigating leopard step lengths with competitor proximity.

Model	R^2	K	AIC_c	Δ AIC_c	Wi
Distance	0.261	9	2129.446	-	0.842
Distance + species	0.262	11	2132.798	3.352	0.158

K = degrees of freedom; AIC_C = Akaike's Information Criterion corrected for small sample sizes; Δ AIC_c = difference between this models AIC_C with the lowest AIC_C value out of all models; Wi = Akaike weight. Random effects variable variances (± SD): leopard ID, 0.616 ± 0.784; competitor ID, 0.001 ± 0.001; encounter ID 0.846 ± 0.916.

Table S20: Model averaged parameter estimates derived from linear mixed-effects candidate models (Table S19) investigating leopard step lengths with competitor proximity. * denotes model parameters that had a significant impact on leopard step lengths.

				Confidence Interval	
Parameter	**Estimate**	**SE**	**Adj. SE**	**Lower**	**Upper**
(Intercept)	2.477	0.423	0.423	1.647	3.307
Distance (400)	0.384	0.197	0.197	-0.002	0.771
Distance (600) *	0.858	0.197	0.198	0.470	1.246
Distance (800) *	0.931	0.197	0.197	0.544	1.317
Distance (1000) *	0.674	0.198	0.198	0.285	1.063
Species (wild dog)	-0.056	0.256	0.257	-1.449	0.744
Species (lion)	-0.005	0.219	0.220	-1.115	1.054

Table S21: Summary of candidate models (Δ AIC_C < 6) of linear mixed-effects modelling output investigating competitor step lengths with leopard proximity.

Model	R^2	K	AIC_c	Δ AIC_c	Wi
Species	0.145	7	2607.063	-	0.847
Distance + species	0.151	11	2611.464	4.401	0.094
Null	0.130	5	2612.585	5.522	0.054

K = degrees of freedom; AIC_C = Akaike's Information Criterion corrected for small sample sizes; Δ AIC_c = difference between this models AIC_C with the lowest AIC_C value out of all models; Wi = Akaike weight. Random effects variable variances (±SD): leopard ID, 0.311 ± 0.559; competitor ID, 0.773 ± 0.880; encounter ID 0.871 ± 0.933.

Table S22: Model averaged parameter estimates derived from linear mixed-effects candidate models (Table S21) investigating competitor step lengths with leopard proximity. * denotes model parameters that had a significant impact on leopard step lengths.

				Confidence Interval	
Parameter	**Estimate**	**SE**	**Adj. SE**	**Lower**	**Upper**
(Intercept)	3.898	0.967	0.969	1.999	5.797
Species (wild dog) *	1.977	1.073	1.075	0.144	4.035
Species (lion)	0.311	0.979	0.981	-1.642	2.300
Distance (400)	0.027	0.125	0.125	-0.318	0.882
Distance (600)	0.049	0.179	0.180	-0.079	1.124
Distance (800)	0.035	0.145	0.145	-0.224	0.976
Distance (1000)	0.009	0.098	0.098	-0.512	0.694

Table S23: Random effect variable variances (± SD) for linear mixed-effects models investigating leopard path metrics following competitor encounters.

		Random Effect Variable		
Metric	**Dyad**	**Leopard ID**	**Competitor ID**	**Encounter ID**
Step length	Leopard-lion	1.084 ± 1.041	1.167 ± 1.080	0.691 ± 0.831
	Leopard-wild dog	0.485 ± 0.696	2.339 ± 0.696	1.698 ± 1.303
	Leopard-cheetah	1.894 ± 1.376	0.655 ± 0.809	1.036 ± 1.018
Tortuosity	Leopard-lion	0.017 ± 0.132	0.035 ± 0.188	0.776 ± 0.278
	Leopard-wild dog	0.001 ± 0.001	0.011 ± 0.106	0.097 ± 0.311
	Leopard-cheetah	0.001 ± 0.001	0.001 ± 0.028	0.003 ± 0.057
Encounter site distance	Leopard-lion	0.621 ± 0.788	0.001 ± 0.001	0.001 ± 0.001
	Leopard-wild dog	0.562 ± 0.750	0.089 ± 0.299	0.711 ± 0.843
	Leopard-cheetah	1.414 ± 1.189	69.826 ± 8.356	0.001 ± 0.001

Table S24: Random effect variable variances (± SD) for linear mixed-effects models investigating competitor path metrics following leopard encounters.

		Random Effect Variable		
Metric	**Dyad**	**Leopard ID**	**Competitor ID**	**Encounter ID**
Step length	Leopard-lion	0.538 ± 0.733	0.001 ± 0.001	1.176 ± 1.329
	Leopard-wild dog	0.094 ± 0.307	0.001 ± 0.001	2.346 ± 1.532
	Leopard-cheetah	0.001 ± 0.001	0.001 ± 0.001	1.897 ± 1.377
Tortuosity	Leopard-lion	0.030 ± 0.174	0.870 ± 0.933	0.140 ± 0.375
	Leopard-wild dog	0.078 ± 0.279	0.172 ± 0.414	0.203 ± 0.451
	Leopard-cheetah	0.036 ± 0.189	0.344 ± 0.586	0.262 ± 0.512
Encounter site distances	Leopard-lion	0.622 ± 0.788	0.001 ± 0.001	0.001 ± 0.001
	Leopard-wild dog	0.001 ± 0.001	0.001 ± 0.001	0.977 ± 0.989
	Leopard-cheetah	0.001 ± 0.001	0.200 ± 0.448	0.001 ± 0.001

CHAPTER 4

Optimal scent marking strategies of a solitary carnivore: boundary and road scent marking in the leopard

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Abstract

Scent marking, where individuals deposit signals on objects in the environment, is a common form of chemical signalling in mammals and is thought to play a critical role in maintaining social organisation within wide-ranging, spatially-dispersed populations. Signallers, however, can incur scent marking costs through mark production, time investment in patrolling and depositing/maintaining mark sites, and increased risk of detection by predators and prey. To mitigate these costs, signallers can adapt spatial patterns of scent marking to increase the probabilities of scent marks being encountered by intended recipients. Relatively little, however, is known of the spatial scent marking placements of many wide-ranging felid species, with most studies focussing on scent mark form and function. Here, we use detailed observational data collected from over seven years of focal follows and high-resolution GPS radio collar data to investigate the spatial placements of scent marks within a leopard population in northern Botswana. We found that leopards exhibited a boundary scent marking strategy by increasing their investment in the maintenance of marking sites in peripheral areas of their home range. We also found that leopards scent marked over four times as frequently and investigated over three times as frequently when travelling on roads than when travelling along natural routes, suggesting that roads may function as hotspots for olfactory information. Compared to leopards from less productive ecosystems, such as the Kalahari, our results (1) suggest that leopards can be highly flexible in their marking strategies, with optimal strategies impacted by the surrounding environment, and (2) provide evidence that human-modifications of the environment now play an important role in facilitating social cohesion within this solitary carnivore.

Introduction

Scent marking, where individuals deposit signals on objects in the environment, is a common form of chemical signalling in mammals and is thought to have functional roles in territoriality and mate acquisition (Gosling and Roberts, 2001; Macdonald and Loveridge, 2010). Whilst the roles of scent marks appear relatively consistent across species, scent marking behaviours vary between and within populations, and across landscapes (Allen et al., 2016a). Signallers incur scent marking costs through mark production, time investment in patrolling and depositing/maintaining mark sites, and increased risk of detection by predators and prey (Gosling and Roberts, 2001; Hayward and Hayward, 2010; Hughes et al., 2012). To mitigate these costs, signallers must make decisions on the optimal placements of scent marks. For example, they can select for areas or objects that increase the probabilities of signals being encountered by intended recipients, as is seen in Eurasian lynx (*Lynx lynx*), which increase scent marking frequencies along routes frequently travelled by conspecifics (Allen et al., 2017; Krofel et al., 2017).

Even though it can be difficult to ascribe actual function to scent marks without considering the responses of receivers, the spatial placements of marks can provide insights into the optimal scent marking strategies for communication (Gosling and Roberts, 2001). The spatial marking strategies employed by signallers are likely dependent on the interplay between a number of factors, including resource distributions (Zhou et al., 2015), home range sizes (Gorman and Mills, 1984), and movement patterns of conspecifics (Krofel et al., 2017). As such, the optimal placements of scent marks can vary considerably across closely related species and also within different populations of the same species. Gorman and Mills (1984), for example, found that the spatial marking strategies of hyaena species varied between ecosystems. Within highly productive landscapes, home ranges were small and scent marks were concentrated along borders: in less productive landscapes, home ranges were larger and hinterland scent marking strategies, i.e. where signals are concentrated within central home range areas, were favoured and more economical than border strategies (Gorman and Mills, 1984).

Human modifications to the environment may also impact optimal scent mark placements by altering the space use of intended recipients (Wilmers et al., 2013). Roads, in particular, may promote scent marking efficiency by increasing scent mark encounter rates if they are preferentially used by intended recipients. In some species, for example, roads channel individual movements because of their positive effects on prey encounter probabilities (Fahrig and Rytwinski, 2009) and landscape permeability (Abrahms et al., 2016). However, although roads are thought to promote scent marking efficiency for some species (Krofel et al., 2017), results have been mixed, and other species have shown similar marking rates when travelling on roads and natural routes (Zub et al., 2003). This suggests that marking on roads carries costs. Disturbance from road traffic may, for example, decrease the persistence of scent marks and thus reduce the overall benefits of road marking. Additionally, it seems likely that dominant competitors will preferentially use roads, while inferior competitors will avoid them (Hayward et al., 2015; Mahon et al., 1998), thereby challenging the ubiquity of individual species responses. Thus, there likely exists a trade-off in the use of roads for scent marking, and its resolution is likely to be species and context dependent (Zimmermann et al., 2014).

Scent marking is widespread amongst felids and plays a critical role in maintaining social organisation within their wide-ranging, spatially-dispersed populations (Wittmer et al., 2014). However, relatively little is known of the spatial scent marking placements of many wide-ranging felid species, with most studies focussing on scent mark form and function (Allen et al., 2017), and relatively little is known of the impact of roads on the scent marking behaviours of felids (but see Krofel et al., 2017).

Leopards (*Panthera pardus*) are solitary large felids, present in a range of habitats across Africa and Asia (Jacobson et al., 2016), including areas with high levels of human-development (Odden et al., 2014). They show intrasexual territoriality, with range overlap varying between populations, and scent marking behaviours that are thought to play a key role in helping them to maintain territories and find reproductive partners (Bailey, 2005; Mizutani and Jewell, 1998). Scent marks are placed throughout territories by both sexes and the observed scent marking behaviours are consistent with those seen in other felids (Allen et al., 2016a; Bailey, 2005). Little is known, however, of how leopard scent marking placements change across ranges and the adaptive significance of such placements, and much of what we do know is based on the identification of scent sites *post-hoc* during spoor tracking surveys (Bothma, 2004; Jenny, 1996; but see Bailey, 2005). Thus, the results are typically biased to easily detectable scent mark types across substrates that leopards can be tracked along, and they are incapable of incorporating information on relative placements within home ranges into the analyses.

Here, we use detailed observational data, collected over seven years of focal follows, and high-resolution GPS radio collar data to investigate the scent marking behaviours of leopards in northern Botswana. We used data from GPS radio collars to delineate leopard home ranges and data collected from focal follows to investigate scent marking frequencies across different substrates and areas of the home range. We also took advantage of the high-resolution data provided by the radio collars to investigate scent mark revisitation times, i.e. the amount of time that elapsed between successive scent mark site visits, which we considered to be a proxy of the time elapsed before scent marks at sites were replenished. Data from two leopard radio collars with spatio-temporal overlap were used in a case-study into the scent marking behaviours of neighbouring competitors within overlapping areas of their home ranges. We assumed that, as with many other felids, leopard scent marks have a functional role in territoriality (Macdonald and Loveridge, 2010), and so we generated a series of hypotheses to consider the optimal spatio-temporal scent marking strategies used by leopards. We hypothesised that scent marking behaviours would occur most frequently and sites would be revisited more quickly within the boundary areas of home ranges rather than the central areas, i.e. that leopards would display a boundary scent marking strategy, since these are the areas where scent marks are most likely to be encountered by intruders. We also predicted that roads would impact scent marking behaviours. Specifically, we hypothesised that leopards would scent mark at higher frequencies on roads and would replenish these signals more often because of the potential of roads to channel conspecific movements.

Methods

Study site

This study was carried out in northern Botswana in the south-eastern region of the Okavango Delta over an area of ~520 km^2. The study landscape was a heterogeneous mix of habitat types, dominated by regions of mopane and acacia-dominated mixed woodlands (Broekhuis et al., 2013). The study area included Moremi Game Reserve and adjacent wildlife management areas that were primarily used for photographic tourism. There were between one and three safari lodges operating within the area throughout the study period, each typically running game drives twice daily, and one permanent research camp, operated by the Botswana Predator Conservation Trust (BPCT). As a result, there was a well maintained network of roads that dissected our study site (Figure 1), which remained relatively consistent throughout the study period, and many resident large carnivores were habituated to vehicles.

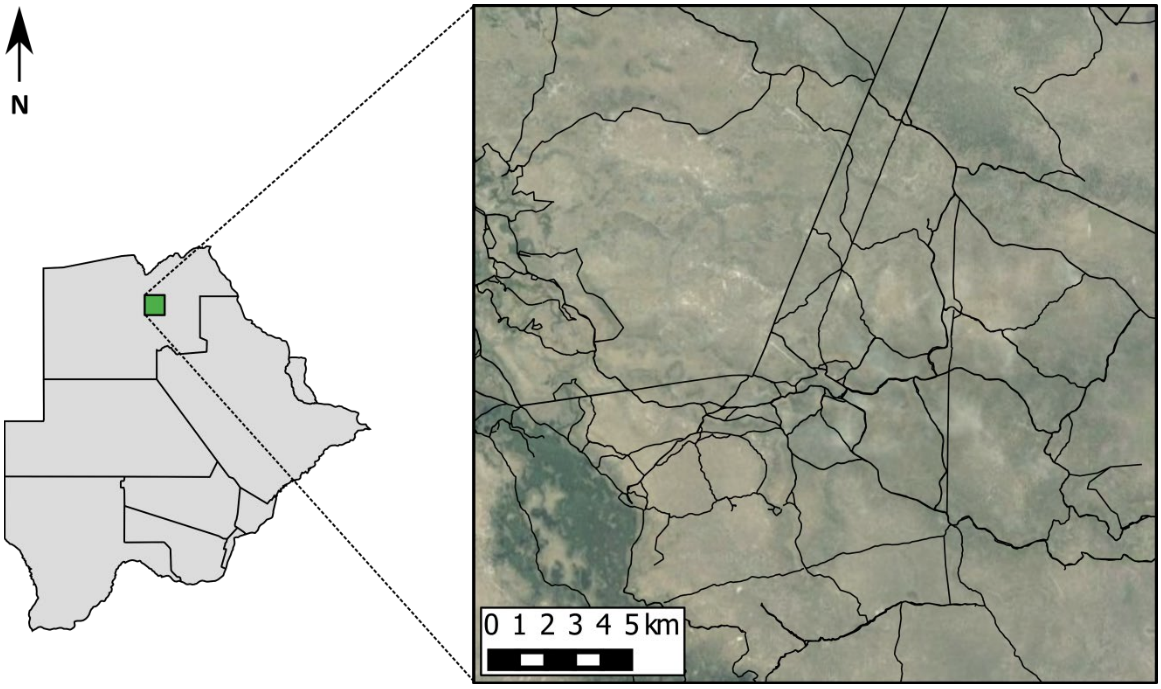

Figure 1: Map of the core study area (right) and its location within Botswana (left). Roads are shown within the core area as solid black lines. The core study area map was created using Google satellite imagery obtained within the QGIS *OpenLayers* Plugin (Kalberer and Walker, 2018).

Behavioural observations

Scent marking data were collected by researchers from the BPCT during focal follows from October 2011 until December 2017. Data were collected on 12 leopards (eight males and four females) that were sufficiently habituated to directly observe without eliciting any obvious changes in behaviour. Leopards were individually distinguishable by their unique rosette pelage patterns (Grey et al., 2013) and were located through a combination of spoor tracking and radio telemetry. Behavioural observations were carried out from within research vehicles at distances of 10–50 m and 20–100 m from leopards when individuals were resting and moving, respectively. Upon locating leopards, sessions were initiated regardless of whether leopards were inactive or active, and in this way, samples were not biased to the collection of active behaviours, such as scent marking. Data were recorded using a critical incident sampling protocol (Altmann, 1974) and collected on Palm TX units using Pendragon Forms (from 2011 until 2015) and on Android smartphones using the KoboToolbox application (from 2015 - 2017). When leopards scent marked or investigated substrates, the mark type (Table 1), substrate marked, and leopard identity were all recorded alongside GPS coordinates.

Table 1: Description of the ten olfactory behaviours recorded during focal sessions.

Category	**Behaviour**	**Description**
Scent marking	Scraping	Alternate raking of hind feet on substrate.
Scent marking	Squat urinating	Squatting over substrate and urinating.
Scent marking	Spraying	Raising tail and spraying back urine onto substrate.
Scent marking	Rubbing	Rubbing face or body onto substrate. Can be done whilst leopard is standing or lying.
Scent marking	Defecating	Squatting over substrate and defecating.
Scent marking	Rolling	Lying and rolling several times on ground. Distinct from rubbing by back and forth rolling. May leave flattened vegetation.
Scent marking	Scratching	Using front claws to scratch substrate.
Investigating	Sniffing	Investigating by placing nose within 0.5 m of substrate and sniffing.
Investigating	Licking	Licking substrate (non-prey) or placing substrate within mouth and chewing for several seconds.
Investigating	Flehmening	Placing face within 0.5 m of substrate and inhaling scent whilst curling upper lip and exposing teeth. Facilitates mark investigation by vomeronasal organ.

From 2015–2017, each marking site within the focal session was also assigned a unique ID, so that combinations of behaviours at the same site could be identified, and the track type (road or natural) that the leopard was travelling along was recorded. Scent marks placed on the same substrate and within 0.5 m of other marks were defined as occurring over existing scent marks, i.e. overmarking. Roads were defined as routes whose regular use by ground vehicles resulted in semi-permanent vehicle signatures on the landscape. Spatio-temporal GPS coordinates were also collected during transitions between leopard behavioural states that were of interest to the wider BPCT project, for example, during transitions between inactive and active behaviours.

Radio collars

Across our study period, we fitted seven male leopards with GPS radio collars developed by the Royal Veterinary College, University of London (for details on collar specifications, see Wilson et al., 2013). For collaring, we selected only mature adult male leopards, using dewlap size as an indicator of age (Balme et al. 2012), in order to minimise welfare issues arising involving radio collars tightening following rapid growth of juveniles. To account for adult growth, we provided two finger widths of space between collars and necks when tightening attachments. Leopards were immobilised by a Botswana-registered veterinarian using a drug cocktail including two or more of ketamine (50 - 200 mg), metodomidine (2 - 5 mg), xylazine (225 - 250 mg) and Zoletil (6 - 250 mg). Whilst individuals were immobilised, radio collars were fitted and vital signs monitored for signs of stress. Reversal drugs, atipamezole (3 - 24 mg) or yohimbine (3 mg), were administered after immobilisation work was complete, and researchers within a vehicle remained with recovering individuals until their movement coordination returned to pre-immobilisation levels. Radio collars were fitted with GPS-inertial measurement units that allowed collars to switch between different sampling frequencies depending on the leopard's activity. GPS sampling frequencies switched between three states: several fixes per second during periods of high acceleration, one fix per five minutes during periods of other locomotion, and one fix per hour during periods of inactivity (Wilson et al., 2013). We were able to collect scent marking data during focal follows for four of the seven radio collared leopards.

Home range, boundary, and overlap area classifications

Kernel utilisation distributions (KUDs) for radio collared leopards were estimated using a bivariate distribution and plug-in bandwidth selection ($H_{\text{plug-in}}$) in the R environment for statistics (R Core Team, 2018) using the packages *ks* (Duong, 2017) and *adehabitatHR* (Calenge, 2006). For justification of this home range estimator see Chapter 2. The 95% isopleths were extracted from KUDs and used to represent individual leopard home ranges. Boundary areas were then visualised by filling holes within 95% polygons and shrinking outer home range boundaries by 1,000 m using the *rgeos* package (Bivand and Rundel, 2017). The 1,000 m definition was based on a preliminary analysis showing that, on average, leopard home ranges overlapped with neighbours by 1,040 m (K. Rafiq, unpublished data). Scent marks within 1,000 m of outer boundaries were thus defined as occurring within boundary areas and those over 1,000 m from boundaries were defined as within central areas. For one pair of neighbouring leopards (CHK & GSE_12), we also had scent marking and GPS data from each individual over the same sampling period. We defined the overlapping area of their 95% isopleths as the 'overlap area' and refer to it as such throughout the remainder of the chapter.

Road marking classification

A geospatial vector file of the main roads within the study area, georeferenced manually by driving roads, was provided by the BPCT. Visual inspection of the map showed that it contained most roads within the area; however, some roads were intermittently present throughout the study period and so were under-represented within the map. Leopard focal session tracks were reconstructed from spatio-temporal coordinates and leopards were defined as travelling on roads when two or more consecutive timestamps were within 15 m of the nearest road. The 15 m threshold was used to account for GPS positional errors and was validated by matching the classification from this threshold against recorded track types of our 2015–2017 data subset. The threshold classification method had 92% accuracy with classifications derived from focal sessions, with visual inspection suggesting that the majority of discrepancies were due to under-representation of roads within the geospatial vector file. Thus, we assumed our 15 m threshold robust enough to assign track types to all pre-2015 data.

Revisitation times to scent marks

We calculated scent mark revisitation times for radio collared leopards by linearly interpolating leopard GPS fixes at one second intervals, creating a 15 m buffer around scent marking site coordinates, and identifying how long after scent deposition or after their previous visit, leopards took to return to the site. This 15 m buffer was chosen to account for GPS sampling errors. Where there were multiple scent marks deposited at the same GPS coordinates within the same session, we used only one scent mark to avoid pseudoreplication. We could not account for non-linear leopard movements between raw fixes. Thus, although there were scent marking sites where we had no revisits, we cannot conclusively say that individuals did not return to them during our sampling period. To account for this, we removed those sites that were not revisited from our dataset and calculated the mean revisitation times to the remaining scents. The visitation times of CHK and GSE_12 to one another's scent marks within the overlap area were also calculated using the methods above.

Statistical analyses

Distances that leopards travelled during focal sessions were calculated from reconstructed tracks and were used to represent scent marking and investigating behaviours as frequencies (per km). We excluded from our analyses sessions with tracks shorter than 100 m to avoid inflated frequencies resulting from short follow distances. For example, if a leopard marked four times over a 20 m distance, this would have given an inflated marking frequency of 200 scent marks/km. For each session, reconstructed tracks were segmented into periods of travel on roads and natural routes, and for those individuals with GPS data, these were further segmented into periods of travel within boundary and central areas of home ranges. Scent mark counts and distances travelled for different segments of the same road/natural routes and boundary/central areas combinations within each focal session were then summed to give overall values for each unique combination for that session.

Due to the data being non-normal and resilient to any change in the distribution after any kind of transformation, the Mann-Whitney U test was employed to compare frequencies between marking and investigating behaviours and to compare behaviour frequencies between sexes. The Kruskal-Wallis test was used to test for differences in frequencies of the top scent marking behaviours against one another. To investigate behaviour frequencies within different home range areas and on different track types, we used a series of linear mixed-effects models using the *nlme* R package (Pinheiro et al., 2016).

Separate models were fitted for overall scent marking and investigating behaviours and for each of the top three scent marking behaviours. Counts were used as responses and an offset of log (track length) was included within models to account for variation in the distances leopards were observed between focal sessions. Leopard identity was included within models as a random effect to control for repeated sampling of the same individuals. To account for unequal variances across leopards and increasing variance with track length, variance structures for leopard identity and session distance were specified and included in the models as weights (Zuur 2009). Linear mixed-effects models were also used to model revisitation times and also included leopard identity as a random effect. Models looking at scent marking and investigating behaviours across different track types used the full scent marking dataset and included track type as an explanatory variable. A data subset that included only the leopards for which we had GPS data for was then used to investigate behaviour frequencies across boundary and central areas and scent mark revisitation times. These models included track type, location within the home range, and an interaction between track type and location as fixed effects. Models investigating behaviour frequencies and revisitation times within the CHK-GSE_12 dyad used a subset of the GPS and scent marking datasets for CHK and GSE_12 that were collected over the same time period. Location (with three levels: boundary, central, and overlap area) was included as an explanatory variable within these models but track type was not included because of limited sample sizes.

An information theoretic approach was used to rank all combinations of models derived from the global using Akaike's information criterion corrected for small sample sizes (AIC_C) (Burnham and Anderson, 2002). Models within six AIC_C units of the highest ranked were retained within a candidate model subset (Richards et al., 2011). A model averaging approach was then applied using the R package *MuMIn* to identify model parameters with a significant impact on the response, i.e. model averaged parameters which were shown to have confidence intervals excluding zero (Barton et al., 2015; Grueber et al., 2011). Candidate models from which model parameters were estimated are included within the supplementary materials (Tables S1– S4). Throughout the results, we report model predicted means, with standard errors.

Results

Overview

We collected data over 786 hours of leopard observations that took place over 491 focal sessions, on eight male and four female leopards, during which leopards were followed for over 143.22 km. We recorded 1172 occurrences of scent marking behaviours and 663 occurrences of investigating behaviours by five male and two female leopards. The majority of focal follow hours occurred in the early evenings (42%, n = 330) and early mornings (26%, n = 204) during peak leopard activity and when light conditions aided data collection (Hubel et al., 2018; Chapter 2), followed by data collected during the day (24%, n = 189) and night (8%, n = 63).

Scraping, spraying, and squat urinating were the most common scent marking types – accounting for 89% (n = 1044) of all scent marks observed (Table 2). Leopards were documented scent marking or investigating nine main substrate types, with grasses, shrubs, and trees accounting for approximately 90% of all marking sites (Figure 2). Most scrape (n = 301) and squat urine (n = 242) scent marks were on grass (81%) and most sprays were on shrubs (52%, n = 195) and trees (34%, n = 127).

Table 2: Summary of the occurrence and mean frequencies (per km) (± SE) of the olfactory behaviours documented during the study.

Category	Behaviour	Occurrence	Behaviour frequency (per km) (mean ± SE)
Scent marking	Scraping	371	3.42 ± 0.41
Scent marking	Squat urinating	298	3.19 ± 0.40
Scent marking	Spraying	375	2.96 ± 0.30
Scent marking	Rubbing	71	0.58 ± 0.15
Scent marking	Defecating	16	0.26 ± 0.09
Scent marking	Rolling	36	0.25 ± 0.07
Scent marking	Scratching	5	0.04 ± 0.02
Investigating	Sniffing	622	5.64 ± 0.58
Investigating	Licking	23	0.19 ± 0.08
Investigating	Flehmening	18	0.10 ± 0.08

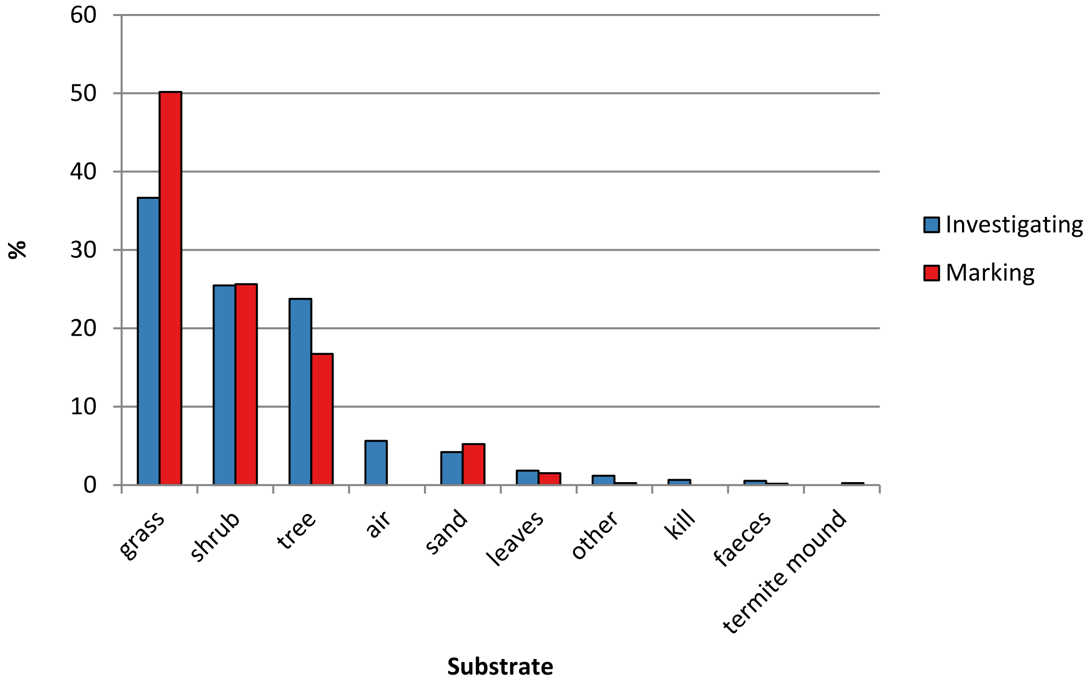

Figure 2: Summary of the percentage of scent marking and investigating behaviours carried out on different substrate types.

Leopards visibly investigated 65% (n = 244) of scent marking sites from our 2015–2017 subset before scent marks were deposited, but 82% of all substrates that were investigated (n = 299) went on to be scent marked (n = 244). Approximately 57% (n =

213) of deposit sites had only one scent marking behaviour carried out at them. Scraping and squat urinating commonly occurred at the same marking sites, with most scrapes (84%, n = 131) involving leopards squat urine overmarking on the site after scraping.

Overall, we documented that leopards scent marked (10.70 ± 1.03 marks/km) nearly twice as frequently as they investigated (5.95 ± 0.64 investigations/km) (Mann-Whitney U = 13,811, $p < 0.001$). Since other felid studies have primarily focussed on scrape, squat urine, and spray marks we also calculated marking frequencies for these behaviours and found that frequencies did not significantly differ between the three scent mark types (Kruskal-Wallis = 0.459, p = 0.795) (Table 2). We also found that male leopards scent marked almost twice as frequently as females, but this was only marginally supported by the statistical test (Mann-Whitney U = 1628, p = 0.050) (Figure 3). Spray frequencies were similar between sexes (Mann-Whitney U = 1321, p = 0.816) and, although mean scraping and squat urinating behaviours were over twice as frequent in males than females, this difference was only significant for squat urinating (Mann-Whitney U = 2926, $p < 0.001$) and not scraping (Mann-Whitney U = 1588, p = 0.075) (Figure 3). There was no significant difference in investigating frequencies between the sexes (Mann-Whitney U = 1478, p = 0.262) (Figure 3).

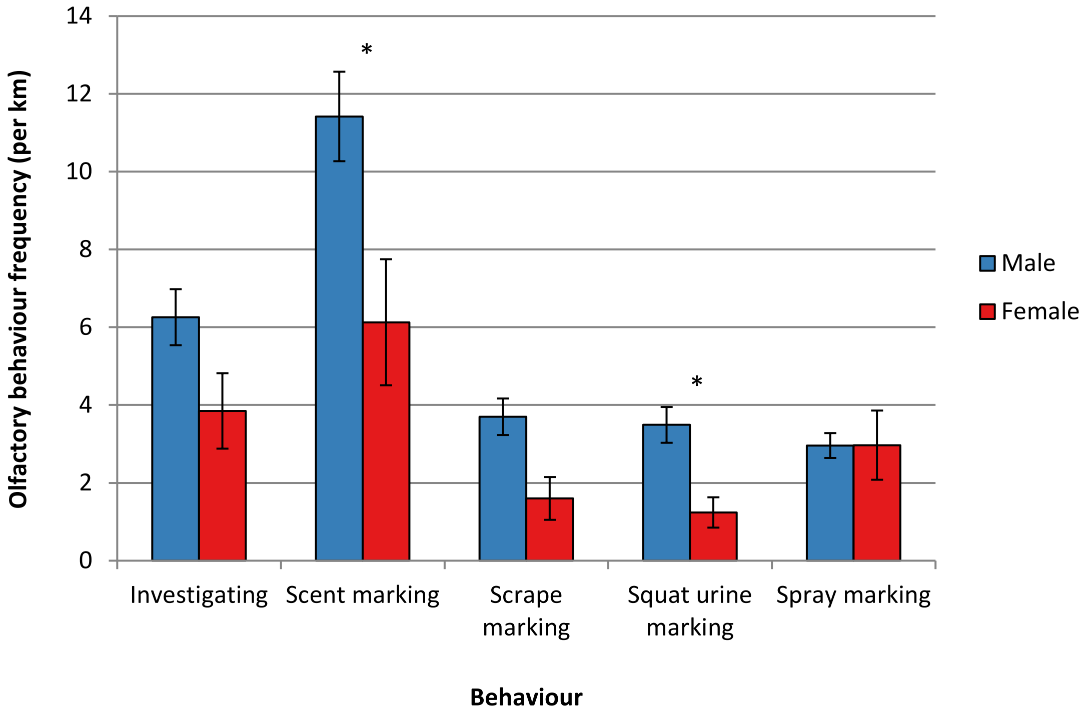

Figure 3: Mean (± SE) investigating and scent marking frequencies (per km) split by sex. * denotes behaviours with significant statistical differences (p ≤ 0.05) in mean behaviour frequencies between the sexes.

Scent marking on roads

Leopards scent marked over four times as frequently and investigated over three times as frequently when travelling on roads than natural routes (Table 3; Figure 4). Scrape and urine scent marks followed the same pattern, with higher marking frequencies on roads than natural routes, but sprays were deposited at similar frequencies across both track types (Table 3; Figure 4).

Table 3: Linear mixed-effects model (Δ AIC_C < 6) averaged parameters predicting olfactory behaviour frequencies across track types. Within the parameters column, parameters are grouped by response variables for each model series (bold). All models included leopard identity as a random effect. Candidate models can be found in Table S1. * denotes parameters with a significant impact on the response.

				Confidence Intervals	
Parameters	**Estimate**	**SE**	**Adj. SE**	**Lower**	**Upper**
All marking					
(Intercept)	1.241	0.179	-	0.494	1.757
Track type (road) *	0.948	0.246	-	0.465	1.431
All investigating					
(Intercept)	0.857	0.099	0.000	0.661	1.052
Track type (road) *	0.537	0.232	0.022	0.172	0.962
Scraping					
(Intercept)	0.533	0.092	-	0.095	0.828
Track type (road) *	0.669	0.169	-	0.337	1.000
Squat urinating					
(Intercept)	0.474	0.085	-	0.290	0.750
Track type (road) *	0.885	0.156	-	0.579	1.190
Spraying					
(Intercept)	0.646	0.075	0.075	0.499	0.794
Track type (road)	0.054	0.119	0.120	-0.153	0.471

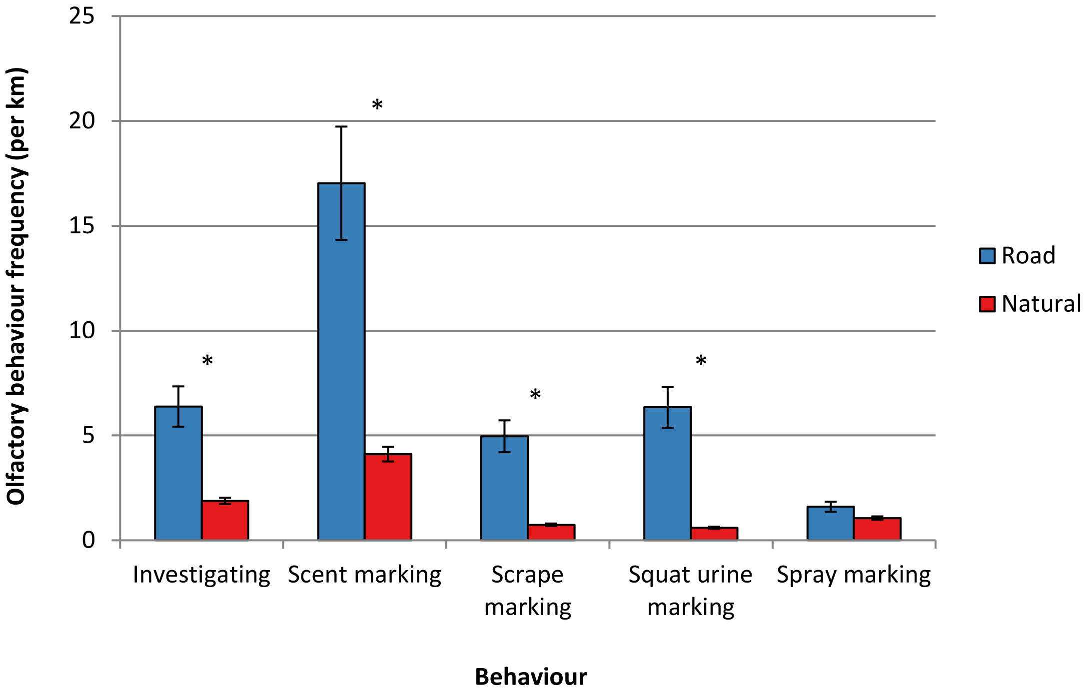

Figure 4: Mean (± SE) leopard investigating and scent marking frequencies (per km) when travelling along roads and natural routes. * denotes behaviours where there is an impact of track type on behaviour frequency (i.e. the track type model parameter's confidence intervals exclude 0).

Scent marking across home ranges

Leopards scent marked in both boundary and central areas of their home ranges and did so at similar frequencies (Table 4; Figures 5–6). Although there was no overall effect of location within the home range on investigation frequencies, there was an interaction between location and track type (Table 4). Specifically, although investigating behaviour frequencies when travelling on roads appeared similar in boundary and central areas, leopards investigated more frequently within boundary than central areas along natural routes (Figure 7). This appears, however, to be a reflection of the relatively small standard errors associated with travel along natural routes relative to those associated with travel along roads. No interaction effect between location and track type was detected on scent marking frequencies.

Table 4: Linear mixed-effects model (Δ $\text{AIC}_C < 6$) averaged parameters predicting olfactory behaviour frequencies across different home range locations and track types. Within the parameters column, parameters are grouped by response variables for each model series (bold). All models included leopard identity as a random effect. Candidate models are presented in Table S2. * denotes parameters with a significant impact on the response.

				Confidence Intervals	
Parameters	Estimate	SE	Adj. SE	Lower	Upper
All marking					
(Intercept)	1.598	0.276	0.279	1.051	2.144
Track type (road) *	0.679	0.306	0.308	0.184	1.249
Track location (boundary)	0.044	0.158	0.160	-0.371	0.640
Track type (road) x track location (boundary)	0.039	0.214	0.215	-0.714	1.572
All investigating					
(Intercept)	0.959	0.163	0.165	0.635	1.283
Track location (boundary)	0.022	0.200	0.202	-0.436	0.497
Track type (road)	0.233	0.290	0.292	-0.327	0.832
Track type (road) x track location (boundary) *	0.668	0.653	0.656	0.192	2.035
Scraping					
(Intercept)	0.774	0.180	0.182	0.417	1.130
Track type (road) *	0.427	0.229	0.230	0.076	0.856
Track location (boundary)	0.018	0.107	0.108	-0.310	0.424
Track type (road) x track location (boundary)	0.044	0.186	0.187	-0.381	1.246
Squat urinating					
(Intercept)	0.664	0.143	0.145	0.380	0.947
Track type (road) *	0.756	0.174	0.177	0.410	1.102
Track location (boundary)	-0.010	0.090	0.091	-0.357	0.291
Track type (road) x track location (boundary)	0.004	0.101	0.102	-0.691	0.808
Spraying					
(Intercept)	0.739	0.136	0.137	0.470	1.009
Track location (boundary)	0.053	0.121	0.121	-0.163	0.483
Track type (road)	0.006	0.096	0.097	-0.342	0.389
Track type (road) x track location (boundary)	0.007	0.078	0.079	-0.525	1.043

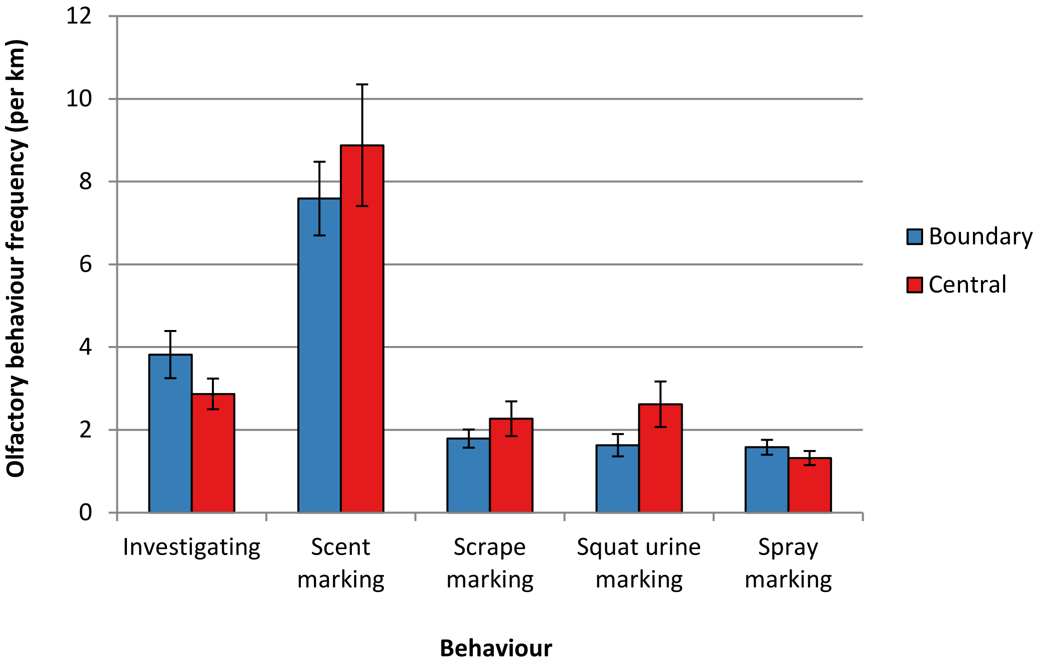

Figure 5: Mean (± SE) leopard investigating and scent marking frequencies (per km) when travelling along boundary and central areas of home ranges.

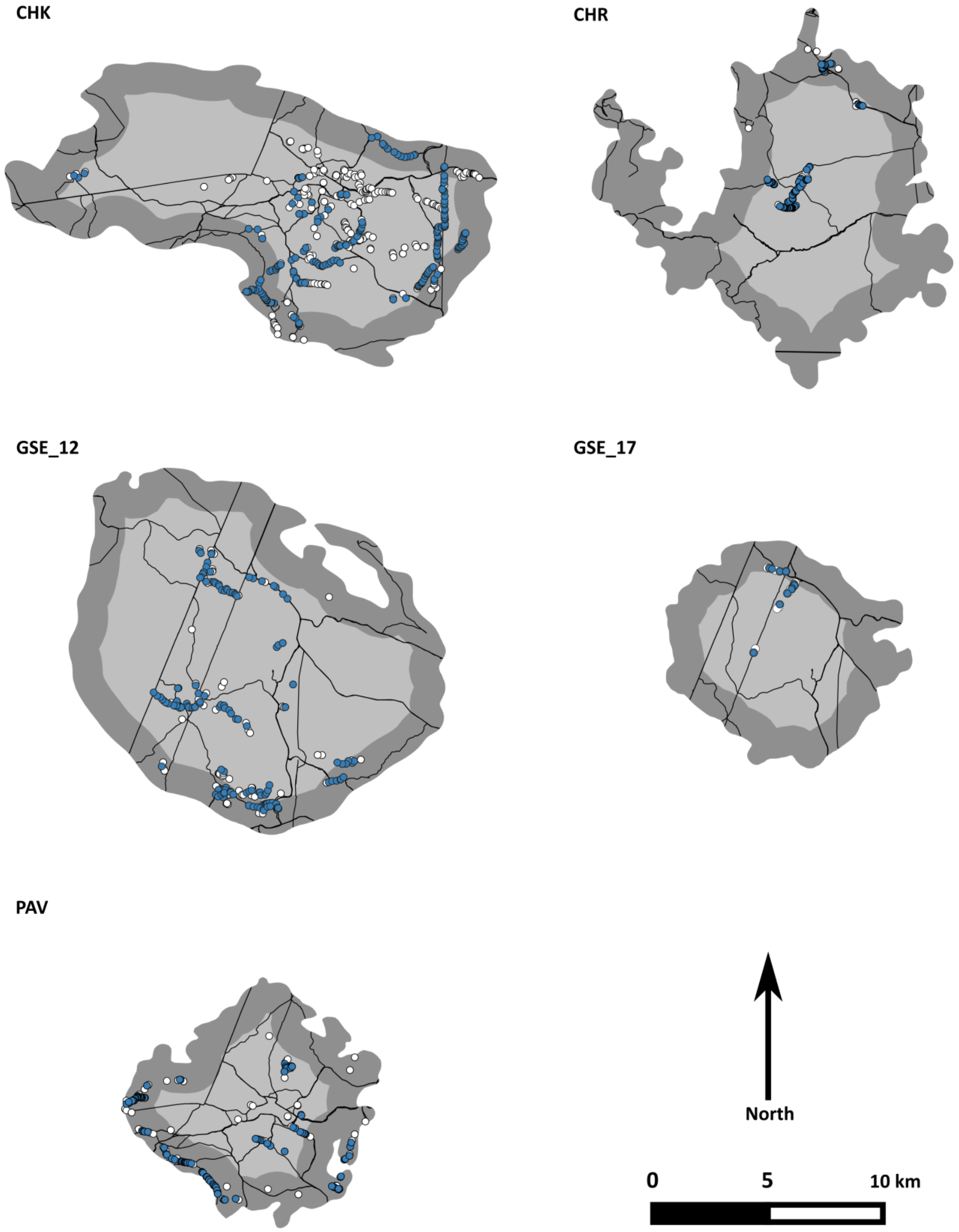

Figure 6: Distribution of leopard follows (white circles) and olfactory behaviours (blue circles) across boundary (dark grey) and central (light grey) areas of leopard home ranges for individuals with GPS radio collars. Roads are depicted as black lines and leopard ID codes are provided in upper left corners of maps.

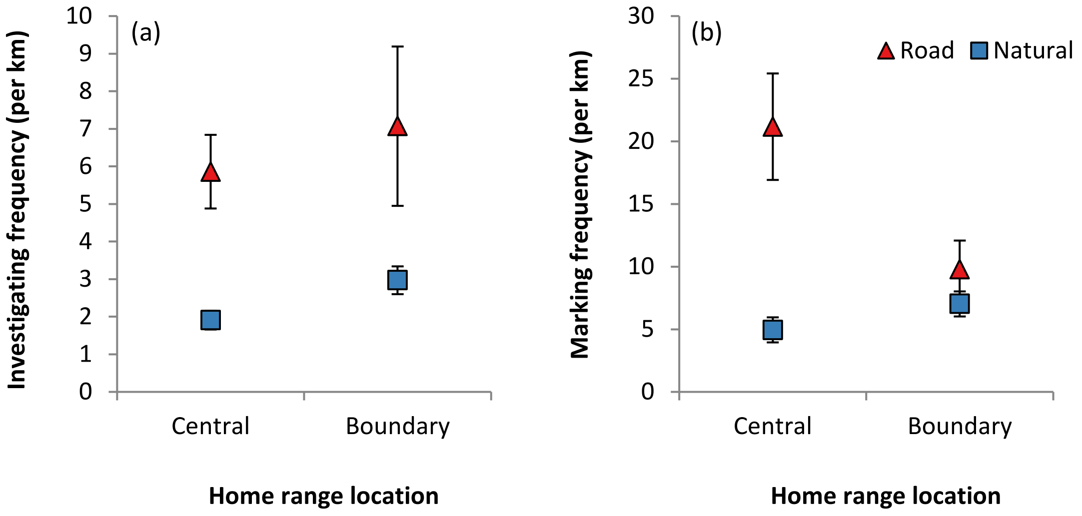

Figure 7: Mean (± SE) leopard (a) investigating and (b) scent marking frequencies (per km) when travelling along road and natural routes in central and boundary home range areas.

When analysing the CHK-GSE_12 dyad, we found that a leopard's location within its home range, i.e. within the central, boundary, or overlap area, had no impact on scent marking frequencies (Table 5). There was, however, an impact of location on investigating, with leopards investigating at higher frequencies in boundary than overlap or central areas of their home range (Table 5; Figure 8).

Table 5: Linear mixed-effects model (Δ AIC_C < 6) averaged parameters predicting CHK-GSE_12 olfactory behaviour frequencies across boundary, central, and overlap areas of home ranges. Within the parameters column, parameters are grouped by response variables for each model series (bold). All models included leopard identity as a random effect. Candidate models are presented in Table S3. * denotes parameters with a significant impact on the response.

				Confidence Intervals	
Parameters	**Estimate**	**SE**	**Adj. SE**	**Lower**	**Upper**
All marking					
Intercept	3.949	1.168	1.192	1.613	6.284
Location (central)	-0.001	0.361	0.369	-2.565	2.535
Location (boundary)	-0.009	0.475	0.485	-3.457	3.239
All investigating					
(Intercept)	0.906	0.303	0.306	0.307	1.505
Location (central)	0.215	0.310	0.313	-0.138	1.070
Location (boundary) *	0.328	0.424	0.427	0.032	1.395
All scraping					
(Intercept)	1.343	0.485	0.495	0.373	2.312
Location (central)	-0.033	0.181	0.184	-1.304	0.629
Location (boundary)	-0.052	0.257	0.261	-1.831	0.762
Squat urinating					
(Intercept)	1.208	0.451	0.460	0.305	2.110
Location (central)	0.007	0.157	0.160	-0.841	0.962
Location (boundary)	-0.054	0.248	0.252	-1.611	0.712
Spraying					
(Intercept)	1.042	0.324	0.329	0.397	1.687
Location (central)	0.060	0.276	0.281	-0.814	1.431
Location (boundary)	0.182	0.474	0.478	-0.408	2.276

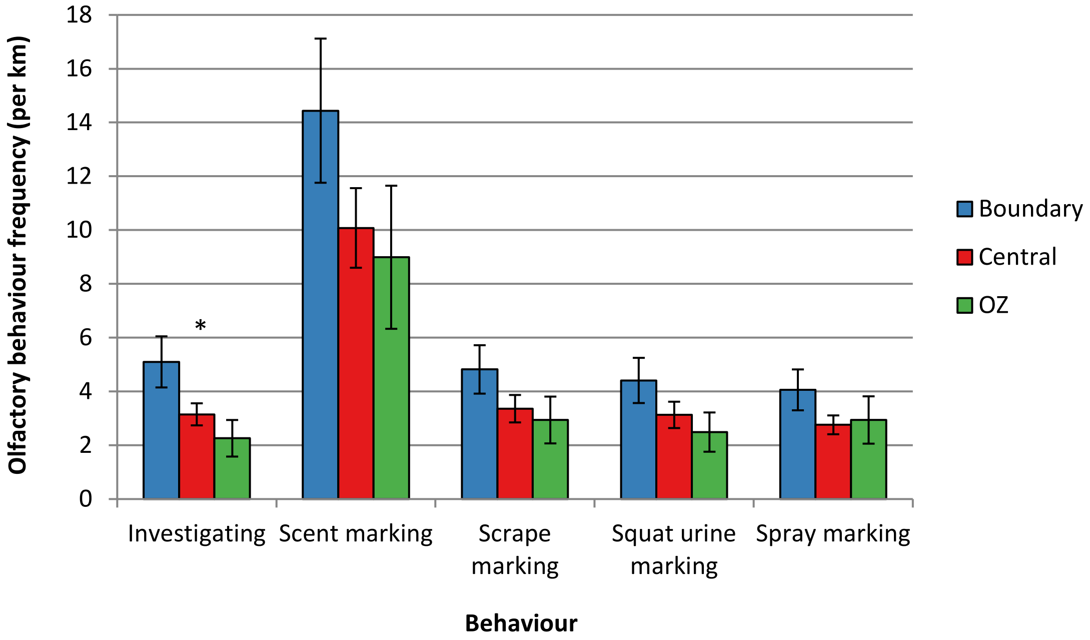

Figure 8: Mean (±SE) scent marking and investigating frequencies (per km) for CHK and GSE_12 when travelling across boundary (non-overlap), central, and overlap areas of their home ranges. * denotes behaviours where there is an impact of home range location on behaviour frequencies (i.e. at least one of the location model parameter's confidence intervals exclude 0).

Revisitation times

On average, leopards revisited scent marks 29.55 ± 0.54 days (n = 215) after they were deposited. Although revisitation times to scent marks deposited on roads (n = 128; 28.64 ± 0.49 days) were statistically significantly shorter than on natural routes (n= 87; 30.90 ± 1.12 days) (Table 6), the scale of the change suggested little biological significance. There was an interaction between track type and home range location (boundary *vs.* central) on revisitation times to scent marks (Table 6; Figure 9). Specifically, the time taken for leopards to revisit scent marks remained similar for scent marks deposited on natural routes in central and boundary areas of home ranges but decreased by 51% when travelling on roads in boundary than central areas (Figure 9).

Table 6: Linear mixed-effects model (ΔAIC$_C$ < 6) averaged parameters predicting revisitation times across different home range locations and track types. Within the parameters column, parameters are grouped by whether models were for all leopards or the CHK-GSE_12 subset (bold). All models included leopard identity as a random effect. Candidate models are presented in Table S4.

				Confidence Intervals	
Parameters	Estimate	SE	Adj. SE	Lower	Upper
All leopard					
(Intercept)	5.800	0.757	0.761	4.309	7.292
Location (boundary)	-0.104	0.645	0.648	-1.373	1.165
Track type (road) *	1.233	0.725	0.727	0.242	2.577
Track type (road) x Location (boundary) *	-1.769	1.144	1.147	-3.806	-0.624
CHK-GSE_2012					
(Intercept)	3.147	0.126	0.127	2.898	3.395
Location (overlap) *	-0.374	0.289	0.289	-0.909	-0.141
Location (boundary)	-0.110	0.171	0.172	-0.519	0.211

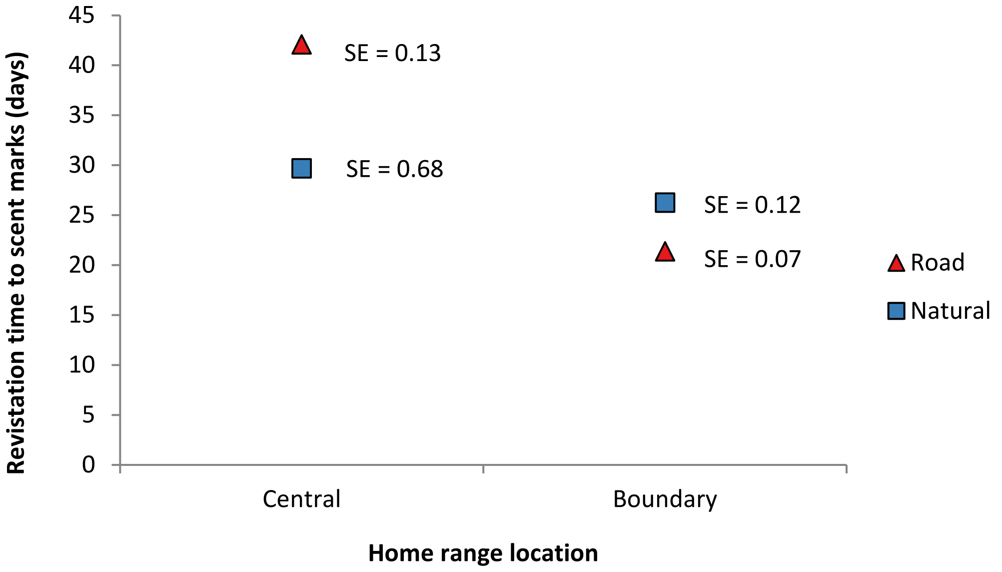

Figure 9: Mean number of days that it took leopards to return to scent marks in different areas of their home range and across different track types. Standard errors are ≥ 0.07 and ≤ 0.68 and so are not visible as error bars, but instead, they are presented alongside each plotted mean.

When analysing the CHK-GSE_12 dataset, we found that leopard revisitation times to their own scent marks were lower in overlap areas (n = 31; 17.73 ± 2.53 days) than in central (n =120; 40.89 ± 3.86 days) and boundary home range areas (n = 55; 35.98 ± 4.46

days) (Table 6). It took on average 25.36 ± 3.51 days (n = 33) for leopards to encounter scent marks left in the overlap area by their neighbour.

Discussion

Leopards adapt their scent marking and investigating behaviours based on their location within their home range and on the medium upon which they are travelling. Although scent marking frequencies remain consistent across home ranges, leopards exhibit a boundary scent marking strategy by revisiting boundary scent marking sites on roads more quickly than scent marks in central areas, presumably for scent site maintenance and investigation. Neighbouring territorial leopards within our study area tended to overlap home ranges by 1,040 m (K. Rafiq, unpublished data). Increased investment of scent marking behaviours at boundaries, particularly within overlap areas, may thus have increased scent marking efficiency and helped to establish social dominance by increasing the chances of active signals being encountered by neighbouring competitors, with scent marking within central areas then primarily aiding mate acquisition. Leopards may thus scent mark at similar rates throughout home ranges to facilitate finding a mate but prioritise maintaining marks at boundary locations because of the potential to lose both territory and long-term mating opportunities. Thus, scent marking at boundaries may facilitate the defence of central home range resources and reduce exploitation competition, e.g. for reproductive opportunities, within central home range areas (Peres, 1989). These results caution against ascribing function to scent marks purely from spatial distributions (Gosling and Roberts, 2001). Future studies would benefit from considering the receivers of signals at different locations, e.g. by camera trapping scent sites (Allen et al., 2016b), and the olfactory information contained within scent marks, e.g. using scent presentation experiments (Jordan et al., 2010), in order to fully appreciate scent mark functions.

Leopards scent marked at frequencies in overlap areas comparable to other areas of their home range but investigated their non-overlapping boundary areas at higher frequencies. Such spatial patterns of scent marking investment may occur if neighbours and strangers compete for different resources and so represent different levels of threat to the investigator (Müller and Manser, 2007). In other words, leopards may investigate at higher frequencies in non-overlapping boundary areas to identify dispersing males looking to establish new territories. That revisitation times to scent marks in the overlap area were lower than elsewhere in the home range also suggests an importance of maintaining familiarity with stable neighbours through regularly maintained scent marks. Whether there are key communication sites within these overlap areas that are used to communicate with conspecifics (e.g. Wittmer et al., 2014) and maintain familiarity is unknown. Camera trap placements at scent marking sites within areas where leopard home ranges overlap could be used to investigate this further.

Consistent with our predictions, leopards had higher scent marking and investigating frequencies when travelling on roads than when travelling along natural routes, suggesting that roads may function as hotspots for olfactory information. This may occur because roads increase mark encounter frequencies, perhaps by channelling leopard movements and increasing landscape permeability, as they do for other species of large carnivores (e.g. Abrahms et al., 2016; Zimmermann et al., 2014). This has implications for the exploitation of these signals by unintended receivers as it increases mark encounter probabilities for all species that use roads as movement corridors (Hughes et al., 2012). Interspecific eavesdropping is particularly common amongst southern African carnivores, with some data suggesting higher occurrences of interspecific than intraspecific overmarking (Apps et al., 2018) and other data suggesting that hyaena latrines have functions as multi-species scent marking sites (Vitale, 2017). Leopards may thus incur costs from increased road marking if signals are encountered by unintended recipients that might alter their behaviours in ways that could be maladaptive to the signaller. For example, predator odours can lead to increased vigilance of prey (Parsons et al., 2018; but see van der Meer et al., 2012), and we anecdotally observed leopards to cover faecal depositions next to kill sites, suggesting that competitors may use olfactory signals to initiate antagonistic encounters. Further, although most human-traffic within the study area was diurnal and so occurred outside of peak leopard activity periods (Hubel et al., 2018; Chapter 2), minimising direct disturbance to scent marking leopards, the costs (or benefits) of traffic on scent mark degradation are unknown. For example, it is unknown whether traffic can help distribute scent marks more widely, i.e. by capturing signals on tyres. Ultimately, the decision to scent mark on roads likely reflects a number of trade-offs in the costs, such as eavesdropping and mark disturbance, and benefits, such as increased conspecific encounter probabilities, of road marking.

Leopards in less productive landscapes, where population densities are lower and home range sizes larger, such as those within the Kalahari (Bothma, 2004; 2012), may adopt different spatial scent marking strategies, as is seen in hyaenas across different ecosystems (Gorman and Mills, 1984). This idea is supported by the observation that our leopard scent marking frequencies were comparable to leopards within tropical rainforests (Jenny, 1996) but were approximately three times higher than leopards within the arid Kalahari (Bothma, 2004). Although each of these studies used different survey methods and focussed on different scent mark types (scrapes and sprays, respectively), comparisons with our results suggest that scent marking frequencies differ between landscapes for, at least, specific mark types. Leopard home ranges within the southern Kalahari were over five times larger than those within our study area (Bothma, 2004; Hubel et al., 2018). Thus, large territories may preclude efficient scent marking at home range boundaries so that Kalahari leopards adopt a hinterland marking strategy and perhaps reduce overall scent marking frequencies (Gorman and Mills, 1984) – this is additionally a likely optimal strategy given that leopards in arid areas occur at lower densities and so have a reduced likelihood of trespassing on conspecific territories (Kingdon, 2013). Additionally, the relative importance of scent marking behaviours in mediating encounters is likely to differ with habitat characteristics. As such, increased visibility within the Kalahari may mean that the role of vision in mediating encounters is more important than in closed habitats and so investment in scent marking behaviours is reduced.

Although we were unable to look at the spatial patterns of female leopard scent marking behaviours because of a paucity of data, we did find evidence for sex-based differences in marking frequencies. Specifically, we found that overall marking and squat urinating behaviours were more frequent in males. This most likely reflects (1) our anecdotal observation that most of our female follows occurred across natural routes and (2) our results that overall marking, scraping, and squat urinating frequencies are significantly lower on this track type. Whether the bias towards female follows on natural routes reflected avoidance by females of roads, and so is likely to impact scent marking strategies, or whether it is a consequence of small sample sizes is unknown. A complementary explanation is that the sex-based differences may reflect sexually dimorphic life histories and reproductive strategies. Males may favour higher scent marking frequencies to advertise perpetual sexual availability, whilst females may use olfactory behaviours primarily for territoriality with higher frequencies exhibited during oestrus, as in other felids (Logan and Sweanor, 2010; Wittmer et al., 2014).

The seven main scent marking behaviours and three investigating behaviours we recorded are consistent with those documented in other solitary felids (Allen et al., 2016a; Smith et al., 1989; Vogt et al., 2014). We also recorded one occurrence of leopards scraping, i.e. alternately raking, with their front feet. To our knowledge this has not been documented in the literature on leopards elsewhere and there may be population specific occurrences of this behaviour, as seen in pumas (*Puma concolor*) (Harmsen et al., 2010; Wittmer et al., 2014). Leopard scrapes were created throughout territories and were often accompanied by urine or faeces, suggesting that scrapes may act as visual cues and aid the discovery of accompanying scent marks (Wittmer et al., 2014). However, given that not all scrapes were accompanied by secondary scent marks, scrapes may also be used to deposit marks from inter-digital glands on the feet (Wilson and Mittermeier, 2009). Multiple scent marks at sites were typically a combination of signals likely coming from subcutaneous or inter-digital glands, such as scrapes and rubs, and those occurring from bodily excretions, such as sprays and urine (Harmsen et al., 2010). Thus, combinations of scent marking behaviours may facilitate scent matching and aid mate selection (for review see Candolin, 2003).

In summary, we have shown that leopards are highly flexible in their scent marking behaviours and that human-modifications of the environment can play a key role in facilitating information transfer within this solitary species. Leopards were shown to exhibit a boundary scent marking strategy through the increased maintenance of boundary located scent marks. Roads appear to play a particularly important role in information transfer, likely functioning as olfactory information hotspots that increase scent marking efficiency and thus help to maintain social cohesion. Our results also suggest a key role of familiarity in maintaining territoriality between neighbouring competitors and show that leopards increase the frequency of investigating behaviours in areas where they are conceivably most likely to encounter same-sex strangers. Thus we provide one of the few studies suggesting a *dear-enemy* effect in a solitary large carnivore, with most studies focussing on this effect within group-living species (Christensen and Radford, 2018). Our results also caution in using spatial data alone to infer scent marking strategies (Gosling and Roberts, 2001). As such, further research on the responses of receivers of scent marking signals and on the olfactory content of scent marks would provide further insights into the function of scent marking behaviours.

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Author contributions

KR and NJ conceived the study; KR collected the majority of the data, performed the analyses, and wrote the manuscript; NJ, CM, MH, contributed to manuscript revisions. AW provided radio collars for this project. JM provided the research infrastructure for field data collection.

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Supplementary Material

Table S1: Summary of candidate models (Δ AIC_C < 6) of linear mixed-effects modelling output predicting olfactory behaviour frequencies across track types. Within the model column, models are grouped by response variables for each model series (bold).

Model	R^2	K	AIC_c	Δ AIC_c	Wi
All marking					
Track type	0.187	9	567.454	-	0.997
All investigating					
Track type	0.207	9	506.709	-	0.947
Null	0.161	8	512.463	5.754	0.053
Scraping					
Track type	0.187	9	567.454	-	0.997
Squat urinating					
Track type	0.171	9	415.449	-	1.000
Spraying					
Null	0.225	8	432.468	-	0.660
Track type	0.230	9	433.793	1.325	0.340

K = degrees of freedom; AIC_C = Akaike's Information Criterion corrected for small sample sizes; Δ AIC_c = difference between this models AIC_C with the lowest AIC_C value out of all models; Wi = Akaike weight. Random effect variable variances can be found in Table S4.

Table S2: Summary of candidate models (Δ AIC$_C$ < 6) of linear mixed-effects modelling output predicting olfactory behaviour frequencies across different home range locations and track types. Within the model column, models are grouped by response variables for each model series (bold).

Model	R^2	K	AIC$_c$	Δ AIC$_c$	Wi
All marking					
Track type	0.194	7	418.094	-	0.613
Location + track type	0.197	8	420.061	1.967	0.229
Location + track type + location x track type	0.201	9	421.932	3.838	0.090
Null	0.138	6	423.083	4.989	0.051
All investigating					
Location + track type + location x track type	0.278	9	372.464	-	0.584
Track type	0.229	7	374.613	2.148	0.199
Location + track type	0.238	8	375.733	3.268	0.114
Null	0.198	6	376.530	4.066	0.076
Location	0.200	7	378.616	6.152	0.027
Scraping					
Track type	0.132	7	339.114	-	0.588
Location + track type	0.133	8	341.235	2.121	0.204
Location + track type + location x track type	0.141	9	342.662	3.548	0.100
Null	0.078	6	343.059	3.945	0.082
Squat urinating					
Track type	0.115	7	318.647	-	0.704
Location + track type	0.115	8	320.923	2.276	0.226
Location + track type + location x track type	0.116	9	323.278	4.631	0.070
Spraying					
Null	0.197	6	328.654	-	0.504
Location	0.203	7	330.224	1.570	0.230
Track type	0.198	7	330.902	2.249	0.164
Location + track type	0.204	8	332.441	3.787	0.076
Location + track type	0.206	9	334.477	5.823	0.027

K = degrees of freedom; AIC$_C$ = Akaike's Information Criterion corrected for small sample sizes; Δ AIC$_c$ = difference between this models AIC$_C$ with the lowest AIC$_C$ value out of all models; Wi = Akaike weight. Random effect variable variances can be found in Table S4.

Table S3: Summary of candidate models (Δ $AIC_C < 6$) of linear mixed-effects modelling output predicting CHK-GSE_12 olfactory behaviour frequencies across central, boundary, and overlap areas of HR. Within the model column, models are grouped by response variables for each model series (bold).

Model	R^2	K	AIC_c	Δ AIC_c	Wi
All marking					
Null model	0.498	4	396.362	-	0.920
Location	0.498	6.00	401.238	4.876	0.080
All investigating					
Null model	0.164	4	190.375	-	0.539
Location	0.226	6	190.691	0.316	0.461
Scraping					
Null model	0.527	4	284.114	-	0.902
Location	0.530	6	288.556	4.442	0.098
Squat urinating					
Null model	0.340	4	260.513	-	0.880
Location	0.349	6	264.507	3.994	0.120
Spraying					
Null model	0.491	4	279.096	-	0.805
Location	0.507	6.00	281.930	2.834	0.195

K = degrees of freedom; AIC_C = Akaike's Information Criterion corrected for small sample sizes; Δ AIC_c = difference between this models AIC_C with the lowest AIC_C value out of all models; Wi = Akaike weight. Random effect variable variances can be found in Table S4.

Table S4: Summary of candidate models (Δ $AIC_C < 6$) of linear mixed-effects modelling output predicting revisitation times across different home range locations and track types. Within the model column, models are grouped by whether models were for all leopards or the CHK-GSE_12 subset (bold).

Model	R^2	K	AIC_c	Δ AIC_c	Wi
All leopard					
Location + track type + location x track type	0.051	6	1063.604	-	0.766
Location	0.015	4	1067.305	3.701	0.120
Location + track type	0.020	5	1068.316	4.712	0.073
CHK-GSE_2012					
Location	0.073	6	631.808	-	0.712
Null	0.044	4	633.618	1.810	0.288

K = degrees of freedom; AIC_C = Akaike's Information Criterion corrected for small sample sizes; Δ AIC_c = difference between this models AIC_C with the lowest AIC_C value out of all models; Wi = Akaike weight. Random effects variable variances (± SD): all leopard, leopard ID, 7.675 ± 2.770; CHK-GSE_2012, leopard ID, 1.501 ± 1.226.

Table S4: Leopard ID random effect variable variances (± SD) for linear mixed-effects models investigating leopard scent marking frequencies across different models (Tables S1-S3).

	Response variables being investigated				
Models	**All marking**	**All investigating**	**Scraping**	**Squat urinating**	**Spraying**
Behaviour frequencies across track types (Table S1)	0.004 ± 0.060	0.002 ± 0.044	0.001 ± 0.035	0.001 ± 0.026	0.001 ± 0.035
Behaviour frequencies across HR locations and track types (Table S2)	0.001 ± 0.058	0.001 ± 0.043	0.002 ± 0.047	0.002 ± 0.040	0.002 ± 0.044
CHK-GSE_12 behaviour frequencies across HR locations (Table S3)	0.091 ± 0.302	0.002 ± 0.048	0.019 ± 0.137	0.012 ± 0.111	0.008 ± 0.090

HR = home range

CHAPTER 5

Citizen-science on safari: tourist photographs as a scalable framework for large carnivore monitoring in protected areas

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Abstract

In the face of rapidly declining biodiversity, protected areas are a cornerstone of conservation. However, most protected areas lack the infrastructure and resources for basic monitoring, with the cost of many wildlife monitoring approaches prohibitive to their long term use. Citizen-science is emerging as a paradigm for facilitating ecological studies; however, questions surrounding cost-effective data collection, accuracy, and processing have limited its adoption into monitoring programs, and within protected areas with wildlife tourism, visitors are often an overlooked source of information. Here, we investigate the potential of using tourist-contributed data to establish robust monitoring programs in protected areas. We implemented a large carnivore citizen-science monitoring program in northern Botswana and compared results from concurrent camera trapping, spoor, and call-in station surveys for lions (*Panthera leo*), spotted hyaenas (*Crocuta crocuta*), leopards (*Panthera pardus*), African wild dogs (*Lycaon pictus*), and cheetahs (*Acinonyx jubatus).* We found that the citizen-science method: (i) was the only method to identify the presence of all target species within the study area; (ii) provided robust density estimates for leopards and wild dogs; and (iii) was the cheapest method to implement and showed the most promise for reducing costs further using machine learning and artificial intelligence advances. Our results suggest that tourist photographs could be used to monitor charismatic fauna within protected areas with wildlife tourism. Considered alongside advances in automated species- and individual-level identification, *via* machine learning and artificial intelligence, an opportunity exists for long-term, low-cost citizen-science powered monitoring programs to aid the management of protected areas.

Introduction

In the face of the Anthropocene's rapid declining of biodiversity, nationally designated protected areas, amounting to 12.9% of terrestrial Earth, are critical for biodiversity conservation (Leverington et al., 2010). The resources available for conservation, however, are limited, and as a consequence, only 40% of these areas are thought to have the infrastructure and resources for basic monitoring (Leverington et al., 2010; Steger et al., 2017). This is problematic as it limits assessment of the effectiveness of protected areas and fails to provide the necessary evidence to identify and prioritise conservation actions (Martin et al., 2007).

From a wildlife conservation perspective, a multitude of methods exist for monitoring wildlife populations, such as camera trapping (Wearn and Glover-Kapfer, 2017), spoor surveys (Winterbach et al., 2016), and call-in stations (Cozzi et al., 2013). Whilst the exact financial and logistical requirements of each sampling method vary, considerable focused survey effort is often required to yield accurate data (Gálvez et al., 2016; Lyra-Jorge et al., 2008; Midlane et al., 2015; Thorn et al., 2010). This makes monitoring difficult to sustain or replicate, which is concerning because understanding long-term trends in population demographics is arguably more important than obtaining isolated measures of demography in a rapidly changing world (Dirzo et al., 2014; Funston et al., 2010).

One emerging paradigm is the use of citizen-scientists in ecological studies to facilitate data collection and processing, which when coupled with emerging technologies could reduce monitoring costs and create a new suite of biodiversity monitoring tools (Newman et al., 2012; Steger et al., 2017; Swanson et al., 2015). Although this approach has facilitated the monitoring of a range of taxa (e.g. Barlow et al., 2015; Biggs et al., 2015; Scott et al., 2018) and has been proposed as a solution to the finite resources available for basic monitoring within protected areas, the potential of this emerging field has yet to be realised (Jepson and Ladle, 2015; Steger et al., 2017). In practice, concerns around the collection, accuracy, and processing of citizen-procured datasets limit its adoption by many conservationists (Pimm et al., 2015), who can be quickly dismissive about the value of such data.

The current paradigm also typically requires citizen-scientists to actively participate in data collection, i.e. contribute to activities beyond their everyday tasks (Tulloch et al., 2013). This limits participation in monitoring programs to those with the time, resources, and motivations to contribute and fails to capture the big data being collected by a wider group as a by-product of other activities (Steger et al., 2017). Within protected areas, for example, often overlooked sources of information are wildlife tourists and guides, who are often especially focussed on encountering and photographing fauna and flora (Lindsey et al., 2007). As such, mass quantities of ecological data are likely being lost, despite the potential applications of big data in ecology and its growing prominence in other sectors of society (Hampton et al., 2013).

Citizen-science programs appear best suited to species that align with the interests and motivations of contributors (Steger et al., 2017). Although multi-species monitoring is advocated when biodiversity maintenance is the goal, such monitoring programs can be expensive to implement (Gálvez et al., 2016; Rovero et al., 2013; Yoccoz et al., 2001). In particular circumstances, surrogate species can be used to address the conservation needs of a wider range of organisms (Di Minin et al., 2016). Large carnivores, for example, often play important structuring and regulatory roles within ecosystems (Ripple et al., 2014). They are also often charismatic species that provide economic benefits associated with tourism and have the potential to act as flagships for conservation

(Haswell et al., 2017; Lindsey, et al., 2007; Ripple et al., 2014), and they thus play critical roles in fundraising and in increasing awareness of conservation issues. This is important because the status and creation of protected areas can be influenced by public opinion, and the economic benefits associated with wildlife can promote positive attitudes of local communities towards conservation (Lindsey et al., 2007; Stoll-Kleemann, 2001; Wang et al., 2006). From this perspective, the sustainable monitoring of carnivore populations within protected areas is critical: it can attract international funding that facilitates the maintenance and conservation of protected areas and the species within them (Dalerum and Somers, 2008).

In this study, we tested whether data extracted from tourist photographs could be used to establish robust monitoring programs within protected areas. To do this, we examined whether photographs taken by tourists could be used to monitor carnivore populations by comparing tourist-contributed data and results to those from traditional carnivore monitoring methods. We implemented a large carnivore citizen-science monitoring program in northern Botswana while conducting concurrent camera trapping, spoor, and call-in station surveys to estimate densities of lions (*Panthera leo*), spotted hyaenas *(Crocuta crocuta*), leopards *(Panthera pardus*), African wild dogs (*Lycaon pictus),* and cheetahs (*Acinonyx jubatus*). We choose to compare citizen-science density estimates against these three other methods as they are the ones commonly used to estimate large carnivore densities (Balme et al., 2009; Midlane et al., 2015; Winterbach et al., 2016)

Our specific objectives were (1) to validate citizen-scientist provided density estimates with those from traditional survey methods and with known minimum reference densities for the study area, and (2) to compare the costs and benefits of all four monitoring approaches. We also sought to collect the citizen-science data in a simple, scalable framework that could be used to expand the project to other regions and taxa. Based on anecdotal evidence that safari guides were frequently encountering large carnivores across a large sampling area and based on advances in spatial capture-recapture models (Russell et al., 2012), we hypothesised that density estimates from the citizen-science method would be comparable to or outperform those from other methods in terms of accuracy and precision. We also hypothesised that as the citizen-science method utilises the existing resources of safari operators and citizen-scientists, at no extra cost to themselves, it would be the most cost-effective method for researchers and conservationists to implement.

Methods

Study site overview

This study took place over a core study area of approximately 670 km^2 located on the south-eastern fringes of the Okavango Delta, Botswana (Figure 1). The study area included Moremi Game Reserve and two adjacent wildlife management areas (NG33 and NG34) that had been subleased by the local community to safari operators for photographic tourism. Three permanent safari lodges were based within the area, each with up to two vehicles departing daily for morning and afternoon game drives, although only one lodge participated in this study. The landscape was a mosaic of different habitat types but was dominated by acacia and mopane woodlands (Broekhuis et al., 2013). All five target large carnivore species were present within the study area with populations under long-term monitoring by the Botswana Predator Conservation Trust (BPCT). As a result of safari and researcher activity, many of the large carnivores within the study area were habituated to vehicles.

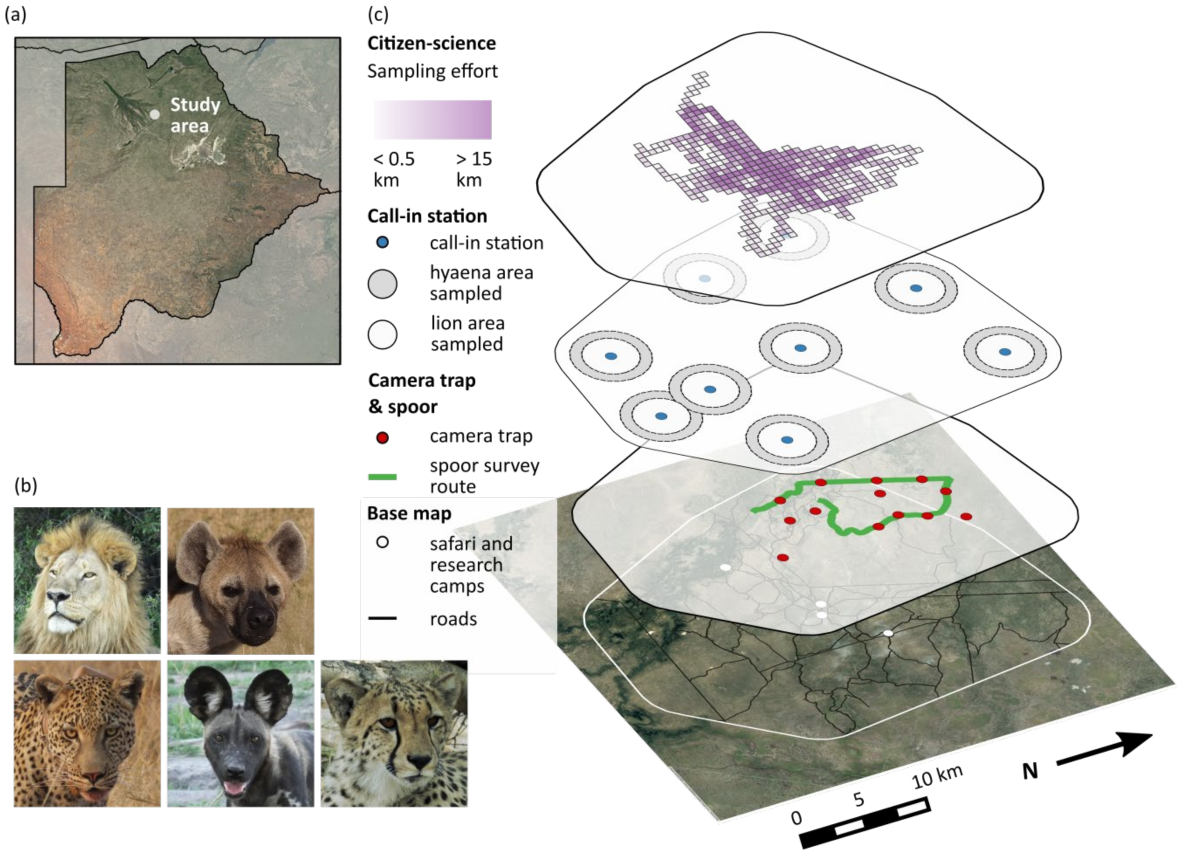

Figure 1: Map of the core study site in the eastern Okavango Delta and the sampling areas of each monitoring method. (a) Study location in northern Botswana; (b) the five study species, from top row, left to right: lion, spotted hyaena, leopard, African wild dog, and cheetah; (c) sampling areas covered during the citizen-science, call-in station, camera trapping, and spoor survey methods. Hyaena image credit: S. Lostrom.

Data collection took place from September 2017 to February 2018 with the exact sampling period and area varying for each monitoring method. Although the rainy season typically occurs from November until March, there were no heavy rains at our study site within the overall data collection period and therefore no change in vegetation composition. Thus, carnivore density estimates from the different methods were unlikely to have been confounded by seasonal variation in resource distributions (Rich et al., 2017) or densities (Hayward et al., 2007; Orsdol et al., 1985). There were also unavoidable differences in the sampling areas of different methods because of limitations imposed by sampling protocols (e.g. camera trap and call-in station spacing) and model assumptions (Cozzi et al., 2013; Royle et al., 2014; Tobler and Powell, 2013). Based on satellite imagery and researcher knowledge of the study area, we concluded that habitat types present within the sampling areas of each method were similar, and given relatively minor differences in sampling area extents, were unlikely to have confounded density estimates.

Citizen-science sampling

Data collection for estimating carnivore densities from tourist photographs took place over a 3.5-month period, from the 6th of September until the 19th of December 2017. During this period, we collected photographs and GPS tracks from every guest group that passed through one of the area's permanent tourist lodges, Santawani. Santawani had a four day guest cycle with guests arriving into the lodge mid-morning of day one and departing early-morning of day four, which was also day one for the next group. Upon arrival at Santawani, our team provided guests with an orientation on carnivore research within the area that concluded with asking if any guests were interested in sharing their photographs with the project at the end of their stay at the lodge. Up to two interested guests were provided with a miniature GPS-logger (i-got-U GT-120) set to automatically record GPS locations at one minute intervals and were asked to keep loggers with them during game drives. Although the features used to identify individuals within each species were mentioned in the orientation, we did not specifically ask guests to take photographs of particular carnivore features at sightings. On the group's last evening at Santawani, we copied guest photographs onto an external hard drive and collected the GPS loggers. Prior to photograph collection, guests were asked to take photographs of a computer screen displaying the current time in UTC. This calibration image was used to adjust camera times to synchronise with the times recorded on GPS logger tracks.

We identified large carnivores to an individual level using unique pelage or whisker spot patterns (e.g. Grey et al., 2013; Pennycuick and Rudnai, 1970), and we assigned latitude/longitude coordinates to individual sightings by matching corrected image timestamps with GPS tracks. Timestamped sightings were then used to pool images from both guests at the same sighting together. This pooled data was used to create unique sightings records for individual carnivores, which were separated into distinct 24 hour sampling occasions. If an individual carnivore was sighted in the morning and afternoon of the same day, we only retained the latitude/longitude location of the morning sighting for our analyses. We only included adult animals (aged > 1 year for wild dogs and > 2 years for other species) for our density estimates (Kingdon, 2013).

We used a series of Bayesian spatially explicit capture recapture (SECR) models, adapted to account for unstructured search-encounter data, to estimate species densities (for details see Muñoz et al., 2016; Russel et al. 2012). We pooled all GPS tracks and overlaid a grid cell matrix (0.5 x 0.5 km) to define our study area (Figure 1c). Carnivores sighted within a grid cell were then allocated to its centre point so that each centre could effectively be considered a discrete trap location, and this allowed sightings to be assigned to specific latitude/longitude coordinates (Muñoz et al., 2016). These grid cells were then surrounded by a 15–25 km buffer that defined an area large enough to include the activity centres of all individuals that could potentially be sampled, i.e. the state space, and encompassed approximately 2,400–4,760 km ^{2} (Royle et al., 2009). Buffer widths were more than 3σ, the spatial scale parameter related to animal movement, as recommended by Royle et al. (2014). Thus, they were assumed as sufficiently large to include all individuals that could have been sampled within the study area (Royle et al., 2016).

Guides did not follow pre-determined routes on game drives for guests; instead, on- and off-road travel routes evolved throughout drives depending on fresh animal signs detected (e.g. spoor), and as such, grid cells had variable sampling intensities for each sampling occasion. To control for this, search effort was included within models as a covariate for encounter probabilities and for each grid cell was defined as the log of the GPS track length within that cell for the sampling period (Elliot and Gopalaswamy, 2017). Sex was also included as a model covariate to control for sex-specific encounter probabilities. For further details on model formulation see Russell et al. (2012). Models were fit using a Markov chain Monte Carlo algorithm and run for up to 150,000 iterations with a burn-in period of up to 15,000, depending on the species (Table S1) (Elliot and Gopalaswamy, 2017). Model convergence was checked using the Gelmin-Rubin diagnostic to ensure that most model parameters were under the 1.20 threshold commonly used as an approximate guideline for convergence (Brooks and Gelman, 1998), and the Bayes p-value was used to check model adequacy (Russell et al., 2012). Models were run within the R environment for statistical computing (R Core Team, 2018) using code modified from Elliot and Gopalaswamy (2017).

Camera trapping surveys

We deployed infrared camera traps (Reconyx® XR6 UltraFire, Reconyx Inc., Holmen, WI, USA) at 13 locations within the study area from the 28th of October 2017 until the 9th of February 2018 (Figure 1c). To ensure systematic coverage of the study area, we placed at least two cameras in each of six adjacent 25 km^2 grid cells. One was placed on the road closest to the centre of the grid cell and the second on the road closest to a predetermined random point within the cell. All cameras were mounted to steel posts 55 cm above the ground to photograph the flanks of passing mammals. We mounted cameras along roads and active game trails to maximize detection probabilities (Cusack et al., 2015). Cameras were programmed to take three high-resolution (eight megapixel) photographs at each trigger event (~1 s trigger speed), day or night, with a delay of 30 s between events. We checked cameras every 5–10 days to check camera functionality, download photographs, and replace batteries.

We collapsed camera trapping data into one week sampling occasions to avoid estimated detection rates close to zero because they can result in estimation problems (Rich et al., 2014) and because of limited numbers of photographic detections. From the adult captures, we created species-specific capture histories that were used to implement SECR models in a maximum likelihood framework within the *secr* package (Efford, 2018) in the R statistical environment (R Core Team, 2018). To define the state space, we used buffers surrounding our camera trapping grid that ranged in size from 9 to 24 km (Table S2). We assumed that each captured individual had an activity centre within the state space and that these centres were uniformly distributed (Royle et al., 2009). We also assumed that the number of photographic detections of individual i at camera station j during sampling occasion k, y_{ijk}, was a Poisson random variable with a mean encounter rate λ_{ijk} (Borchers and Efford, 2008; Royle et al., 2009). We modelled λ_{ijk} using a half-normal decreasing function of the distance between the camera trap and an individual's activity centre, dependent on $g0$, the baseline encounter rate, and σ. We assumed $g0$ and σ were constant across sampling occasions. For each species, we then fit models by maximizing the full likelihood.

Spoor surveys

From the 2nd to the 18th of November 2017, we conducted spoor surveys along a 33.5 km transect within the core study area (Figure 1c). We surveyed alternating halves of the transect by identifying and recording the spoor for each of the target five large carnivores. We repeated each of these two segments five times for a total seasonal transect distance of 167.5 km. For every 4.5 km^2 of sample area, 1 km of transect was surveyed, creating a high penetration density (the ratio of kilometres of transect surveyed to total sample area) of 1:4.5. Roads were driven at < 15 km per hour, and an experienced local tracker assisted in identifying and recording the location, travel direction, species, and age (adult or juvenile) of encountered spoor. Spoor/track incidences were considered as independent observations only if no similar conspecific tracks were found going in the same direction (± 90°) along the transect within 500 m of the ending point of the previous incidence. Multiple individuals present within the same group of tracks were considered as a single track incidence (Funston et al., 2010), i.e. the tracks of six individuals walking in the same direction, along the same section of road were considered as one track incidence and not six.

To calculate densities, we followed the approach outlined by Funston et al (2010) and Winterbach et al (2016). For each species, track metrics (including mean track density, standard error, and confidence intervals) were calculated by bootstrapping, over 20,000 iterations, actual distances between independent adult track incidences and adjusting bootstrapped values by species-specific calibration factors that had been derived and validated using independent data (Funston et al., 2010; Winterbach et al., 2018). Track densities were then used to estimate carnivore densities using the formula: *carnivore density = track density/3.26* (Winterbach et al., 2016). This formula has been shown to most appropriately model African large carnivore densities from track counts on sandy substrates in habitats similar to our study area, i.e. where carnivore densities are > 0.27 carnivores/100 km^2 (Winterbach et al., 2016).

Call-in station surveys

We followed the sampling protocol of Cozzi et al (2013) across nine call-in station sites from the 3rd October to the 10th November 2017 to estimate lion and spotted hyaena densities (Figure 1c). Each site was positioned near the intersection points of a rectangular 7×7 km grid to minimize the chances that an individual could hear playback sounds from more than one call-in station at the same time (Cozzi et al., 2013; Mills et al., 2001). Lions and spotted hyaenas respond differently to calls of conspecifics *vs.* competitors, and so we conducted separate lion and spotted hyaena call-in station surveys at the same nine sites, which were separated by one month to minimise potential habituation (Cozzi et al., 2013). We used the same calls as Cozzi et al. 2013, played through a Tannoy CPA 12 speaker connected to a Boss CXX1002 amplifier, to attract lions and spotted hyaenas to call-in stations. For lions, we played a 10 minute recording consisting of distress calls of buffalo (*Syncerus caffer*), hippopotamus (*Hippopotamus amphibious*), and wildebeest (*Connochaetes taurinus*), conspecifics roaring, and hyaena calls. For spotted hyaenas, we played the distress sounds of a wildebeest and different hyaena vocalisations over a six minute period. See Cozzi et al. 2013 for detailed call-in station playback protocols.

We calculated site-specific density estimates by dividing the number of adults that approached the call-in stations by the area sampled around each station (12.6 and 27.0 km^2 for lions and spotted hyaenas, respectively) and the species-specific likelihood of animals approaching (0.6 and 0.9 for lions and spotted hyaenas, respectively), both of which were calibrated by Cozzi et al. (2013). These were then averaged for each species to provide overall lion and spotted hyaena density estimates for the study area.

Minimum Reference Densities

To compare the accuracy of our various density estimates, we needed to know the true densities of carnivores within the study area. Since this is rarely possible in unfenced systems, we calculated minimum reference density estimates for the citizen-science sampling area using study system knowledge of BPCT researchers and radio collar-derived GPS data that, for most individuals, were collected over the same approximate time period as this project. Specifically, we had near full GPS coverage of the sampling area for resident lion groups (n = 4), African wild dog packs (n = 3) and for adult male leopards (n = 4). Since for many of these individuals/groups their home ranges included areas outside of the sampling area, we calculated the proportion of each collar's GPS fixes that occurred within the sampling area and then multiplied this by the number of adults within that social group. This gave us an adjusted count of individuals from that social group occurring within the area (Ferreira and Funston, 2010; Stander, 2004). For each group, we also extracted the 95% isopleths from kernel utilisation distributions, created using the $H_{\text{plug-in}}$ smoothing factor, and used these to represent home ranges. We then calculated the proportion of the home range that overlapped the sampling area and created a metric ($T_{\text{GPS-poly}}$) for how this value was related to the proportion of fixes within the sampling area by dividing the home range proportion by the GPS fix proportion.

For lions and leopards, there was one region within the sampling area where we had no radio collared territorial males. We used mean home range sizes for lion coalitions (K. Rafiq, unpublished data) and male leopards (Hubel et al., 2018), within our study area, to estimate the location of a home range polygon with minimal overlap with other same-sex residents in the study area. Since we could not calculate the proportion of GPS fixes within the sampled area for these polygons we instead used a proxy for time spent in the area. To do this, we multiplied the home range polygon's overlap with the sampled area by $T_{GPS\text{-}poly}$. We knew from BPCT sightings data that the male coalition within that area was composed of three males and so the proxy value for time spent in the area for the unknown male coalition was multiplied by three. Although there were no radio collared female leopards over the study period, we knew from historical BPCT GPS data that male leopard home ranges were approximately 3.1 times the size of female home ranges. We thus estimated the number of female leopards within the area as 3.1 times the number of males. Since prey density can impact home range size (Hayward et al., 2009), we used long-term herbivore survey data to confirm that prey densities had remained unchanged from 2008 (when the GPS data was collected from which female home ranges were calculated) to 2017 (K. Rafiq, unpublished data)

For each species, the GPS-derived counts of individuals within the area were then summed and adjusted to individuals per 100 km^2 to provide minimum reference density estimates for our study area. We had no radio collared spotted hyaenas within our study area during the study period, and so we used the mean of the results of three previous monitoring studies as our minimum reference density estimate (Cozzi et al., 2013; Rich, 2016; Vitale, 2017). We suggest that, since all three studies produced similar density estimates, the mean of these values is our best indicator of true spotted hyaena density within the area.

To test whether each of our survey methods provided robust estimates of carnivore densities, we then looked at whether their 95% confidence intervals for each species encompassed the species' minimum reference density and used this as a proxy for accuracy. Species percentage confidence limits for each method were used to calculate precision with:

$$\frac{((Upper\ 95\ CI - Lower\ 95\ CI)}{2} \times \frac{100}{mean}$$

where the confidence intervals (CI) and the mean are species-specific (Ferreira and Funston, 2010). Lower percentage confidence limits indicated higher levels of precision.

Comparing method costs

Since we were specifically interested in the costs of implementing these surveys to researchers or wildlife managers, we did not include safari operational costs (e.g. safari vehicle, fuel, or guide costs) into our analyses. Ultimately, these are costs that would have been incurred by safari operators irrespective of our involvement. We monetised and compared survey method costs ($ USD) incurred across four categories: (1) data collection, (2) data processing, (3) consumables, and (4) equipment. We monitored research hours spent on data collection and data processing and assigned costs by multiplying hourly investments by $4.68. This value was calculated as the mean hourly wage + *per diem* paid to field assistants by Botswana NGOs, who provided this data to the project under anonymity. Equipment common to all surveys, e.g. field vehicles, were not included in the cost analyses, but consumables, such as fuel, were calculated because costings were likely to differ between each method (Table S3). Time investments and consumable use were monitored for a portion of each method's sampling period and this was extrapolated to estimate the overall investments required for each. For example, if weekly time investments on camera trapping activities were 20 hours, this was multiplied by the number of sampling weeks to calculate overall camera trapping time investments.

Detection per unit effort

To consider the impact of different sampling intensities, we compared species-specific detections per unit effort (DPUE) amongst methods. For each method, we defined species-specific DPUE as the total number of detections/total time spent capturing detections. Whether sightings with multiple individuals at the same encounter were grouped or counted as separate detections depended on how each method treated grouped individuals within its analysis. Within the citizen-science, camera trap, and call-in station analyses, encounters to the individual level were distinct, whilst for spoor surveys, clustered tracks (separated by < 500 m and traveling in the same direction) of the same species were grouped as one detection. Time was chosen as the measure of unit effort because it was universally applicable to each method. For example, for camera trapping, total time spent capturing detections was equal to the total number of camera trapping hours, and for spoor surveys, it was the total time spent driving transects.

Results

Overview

We collected 25,062 photographs across 78 out of 104 potential sampling days (with missing days representing lodge periods with no guests) from 26 guest groups. Thirty percent (7,436 images) of all photographs were of large carnivores and were taken across 136 encounters. These amounted to 632 records of unique carnivore sightings (all age classes) from all sampling days (Table 1). In contrast, large carnivores were detected 194 times during camera trapping, 178 times (independent track incidences) during spoor surveys, and 15 times during call-in stations (Table 1). Recorded large carnivore species diversity differed by survey method, with the citizen-science method being the only one to detect cheetah presence within the study area (Table 1). The citizen-science and camera trapping surveys were the only methods which allowed individual carnivore identification. The citizen-science method provided the highest classification of carnivores to the individual level, with an average of 95% of all carnivores present at sightings reliably identified (Table 1). In turn, this provided 286 records of adults to be used in SECR models. In contrast, 63% of carnivores were identifiable to the individual level from camera trap images, dipping as low as 37% for some species (Table 1).

Table 1: Total number of carnivores sighted (for citizen-science, camera trapping, and call-in stations) and track incidences (for spoor surveys) for each monitoring method and the % that were identifiable to the individual level. Note, these values are not standardised by effort.

	Citizen science		**Camera trapping**		**Spoor survey**		**Calling station**	
	Sighted	**ID (%)**	**Sighted**	**ID (%)**	**Sighted**	**ID (%)**	**Sighted**	**ID (%)**
Lion	423	91.25	57	64.91	15	-	3	-
Hyaena	20	85.00	52	80.77	109	-	12	-
Leopard	40	100	62	37.10	46	-	-	-
Wild dog	145	100	23	69.57	8	-	-	-
Cheetah	4	100	-	-	-	-	-	-
Overall	632	95.25	194	63.09	178	-	15	-

Density estimates

Our minimum true reference densities (individuals/100 km^2) were 7.50 lions, 14.90 hyaenas, 9.10 leopards, and 4.84 wild dogs. Density estimates were available for the most species using data from citizen-science and spoor survey methods, with only cheetah densities missing because of limited sightings. In contrast, call-in station and camera trapping surveys were only able to calculate densities for two and three species, respectively. Spoor surveys provided accurate density estimates for three species, i.e. with their confidence intervals encompassing minimum species reference densities, camera trap and call-in station method confidence intervals encompassed reference densities for two species, and the confidence intervals of the citizen-science method encompassed the reference density of one species (Figure 2). However, given that reference densities had no measure of uncertainty associated with them and given that the wild dog citizen-science upper confidence limit (CI_{95} = 0.04, 4.62) was only 0.22 units from the reference density, we assumed that the citizen-science method also provided an accurate measure of wild dog density, i.e. it provided accurate densities for two species in total. Precision was highest for estimates derived from the citizen-science method, followed by those derived from spoor surveys (Table 2). The citizen-science models also provided estimates for non-density parameters, including sex ratios and baseline encounter probabilities (Table 3). For all species, except cheetah, detections per unit effort were the highest for spoor surveys, with detections per unit effort 2–66 times larger than the next closest method, and were lowest for the camera trapping method (Table 4).

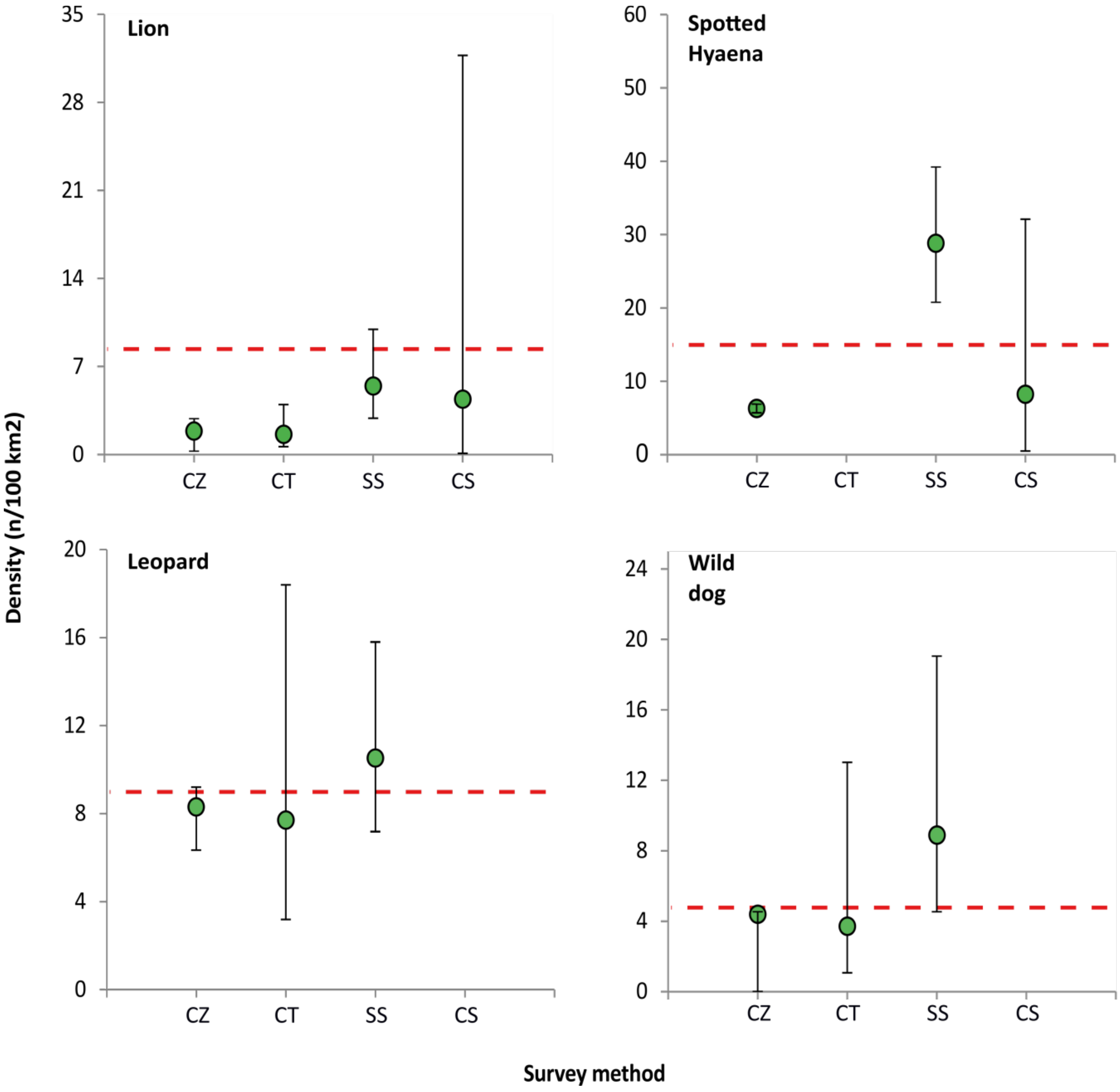

Figure 2: Summary of species density estimates from the citizen-science, camera trapping, spoor survey, and call-in station methods. Mean density estimates are provided alongside 95% confidence intervals. For each species, minimum reference densities are shown as a red dashed line.

Table 2: Precision values for lion, spotted hyaena, leopard, and wild dog density estimates derived from citizen-science, camera trapping, spoor survey, and call-in station methods.

	CZ	CT	SS	CS
Lion	61.39	104.69	64.64	360.03
Spotted hyaena	4.34	-	30.06	194.99
Leopard	17.52	98.77	38.80	-
Wild dog	53.01	161.49	84.24	-

Table 3: Mean and standard deviation (in brackets) posterior parameter estimates from SECR models used to estimate lion, spotted hyaena, leopard and wild dog densities from tourist photographs. Definitions for each of the parameters can be found in Table S4.

	N_s	σ	β_{sex}	β_{eff}	λ_0	ψ	ψ_{sex}	ϑ
Lion	96.886 (46.831)	2.831 (1.126)	4.077 (1.518)	3.875 (0.273)	< 0.001 (< 0.001)	0.190 (0.092)	0.374 (0.244)	0.764 (0.124)
Spotted hyaena	325.954 (130.998)	0.227 (0.264)	17.002 (12.215)	2.687 (0.920)	< 0.001 (< 0.001)	0.642 (0.258)	0.236 (0.369)	0.756 (0.141)
Leopard	203.029 (58.306)	3.280 (5.628)	1.264 (0.932)	0.784 (0.378)	< 0.001 (< 0.001)	0.660 (0.190)	0.726 (0.210)	0.835 (0.124)
Wild dog	207.178 (58.882)	0.901 (0.107)	0.636 (1.168)	4.273 (0.322)	< 0.001 (< 0.001)	0.401 (0.116)	0.315 (0.147)	0.523 (0.028)

Table 4: Species-specific detections per unit effort (hours) for citizen-science (CZ), camera trapping (CT), spoor survey (SS) and call-in station (CS) methods.

	CZ	**CT**	**SS**	**CS**
Lion	0.078	0.002	0.278	0.049
Spotted hyaena	0.006	0.002	2.019	0.196
Leopard	0.013	0.002	0.852	-
Wild dog	0.072	0.001	0.148	-
Cheetah	0.003	-	-	-

Comparisons of effort

Implementing the citizen-science monitoring program cost less than all of the other survey methods. It was 96.87% and 54.42% cheaper than camera trapping and call-in station surveys, respectively, but was negligibly (1.17%) less expensive than spoor surveys (Figure 3). We also calculated camera trapping costs with less expensive camera traps (Browning Strike Force HD Pro; unit cost: $159.95) and with no equipment costs (under the assumption that all equipment could be borrowed). In these scenarios, total camera trapping costs were $3,869.74 and $1,015.83 respectively, and the camera trapping method was 12.92 and 3.39 times more expensive than the citizen-science survey.

Excluding camera trapping, researcher time investments were the biggest cost associated with each method. In spoor and call-in station surveys, relatively little overall researcher time investments were spent on data processing, 9.26 % and 1.60 %, respectively, compared to data collection, whilst in the citizen-science and camera trapping surveys 73.51 % and 33.60 % of researcher time investments, respectively, were on data processing.

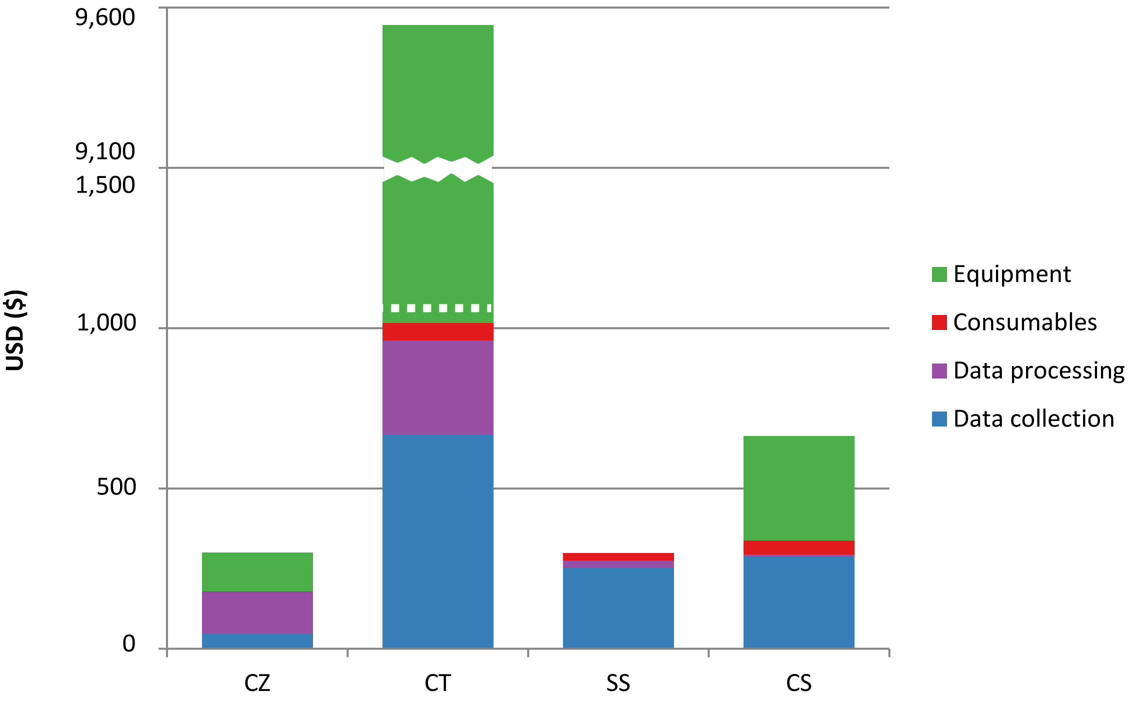

Figure 3: Overview of the costs in implementing each survey method (CZ = citizen-science; CT = camera trapping; SS = spoor surveys; CS = call-in stations) over the course of the study. The white dashed lion across camera trapping costs denotes the total cost if no equipment purchases are required.

Discussion

Density estimates

The citizen-science method was the cheapest monitoring program to implement, was the only method to detect all five large carnivores, and provided the same number of accurate density estimates as most of our other carnivore monitoring methods. The citizen-science method performed particularly well in estimating leopard and wild dog densities, with narrow confidence intervals encompassing (or close to encompassing) minimum reference density values. Lion and spotted hyaena densities were poorly represented by most methods, apart from spoor surveys for lions. Specifically, estimates showed either precise confidence intervals that did not encompass the reference densities or extremely large confidence intervals that did encompass reference density values but whose usefulness can be questioned because of their potential to obscure population trends over time. Further, whilst spoor surveys did provide accurate species densities for a larger number of species than the citizen-science method, estimates were also often accompanied by larger confidence intervals, and as such, this method may also face challenges in detecting changes in population demographics over time. This is complicated by the fact that spoor surveys do not account for species detectability, which can change with a range of factors (e.g. habitat density, species characteristics, and weather) that can vary across space, time, and species (Guillera-Arroita, 2017; Hayward and Marlow, 2014; Ruiz-Gutiérrez and Zipkin, 2011). As such, this may also impact the ability of spoor surveys to detect population trends over spatio-temporal scales useful for conservation (Hayward and Marlow, 2014).

The performance of the citizen-science method in estimating lion and spotted hyaena densities may reflect the total number of species captures (e.g. spotted hyaena captures at independent sites were low) and the relatively small sampling area. This is promising because such issues are simple to overcome with increased citizen-science participation within monitoring areas. As the number of independent samplers, e.g. from different vehicles and lodges, within an area increases, so likely too will the total sampled area and the number of captures, the latter reflected by the positive β_{eff} parameter outputs associated with all models. Of course, this large-scale participation of citizen-scientists presents its own set of challenges (Steger and Butt, 2015; Tulloch et al., 2013); however, certain aspects of our approach, e.g. the use of data collected as a by-product of other activities, make it particularly well suited for scaling (see sections from '*passive data collection*' to '*the role of wildlife safari operators*'.

Beyond densities

Cheetah presence within the study area was only detected through tourist photographs. This may reflect the underlying processes by which data is generated by the different methods and has broader implications for the applications of the data beyond density estimates. The citizen-science method is particularly well suited to detecting the presence or absence of charismatic fauna because species can be encountered across the sampling area with search routes evolving in real-time based on fresh signs within the environment. Consequently, this also addresses concerns of biased density estimates arising from using data derived purely from trail-based surveys, e.g. changes in detectability on trails may not correspond with increased species densities but may instead reflect a species' willingness to use the trails based on other factors (see Hayward and Marlow, 2014). In the citizen-science method, species detection is also facilitated by the collaborative search-efforts of tourists and guides, which provide detection radiuses conceivably larger than for other methods. Indeed, of the methods that did not rely on indirect measures of species presence, i.e. spoor surveys, citizen-science detections per unit effort were highest for all species, bar spotted hyaena. Thus, for species with low encounter probabilities or those that cannot be individually identified for capture-recapture models, tourist photograph presence-absence records and additional information gathered from directly observing individuals, e.g. on prey species and group compositions, may still provide a range of ecological and conservation opportunities (Caravaggi et al., 2017). For example, occupancy can be linked with habitat covariates to provide insights into key resources or habitat features (Karanth et al., 2011; Steenweg et al., 2016), and direct observations can aid the monitoring of endangered species by providing wildlife managers and rangers with information on the location, status, and health of heavily persecuted groups. As an example of the latter, this project provided Botswana's anti-poaching patrols with information on rhino sightings.

Sampling intensity caveats

Monitoring methods differ in the processes that generate data, attributes of the collected data, and their statistical approaches. As such, comparisons between methods may be considered contentious. Although it could be argued that a similar number of detections, through increased sampling effort, for each method are a prerequisite for their comparison, in practise, the finite resources available for conservation limit the practicality of such requirements. Assuming detections increase linearly with effort, for some species 72 times as many camera traps, for example, would have been required for a comparable number of detections with tourist photographs. In any case, increased sampling efforts would also have increased implementation costs and, given that the citizen-science method was already the cheapest to implement, would likely not have changed the cost-benefit outcome for wildlife managers. Further, although implementing the citizen-science survey was similar in cost to the spoor survey, it provided additional layers of information (e.g. on group compositions and population demographics) than the spoor survey's presence-absence records. The framework by which the citizen-science data was collected also presents opportunities to reduce implementation costs even further and to scale data-collection over larger areas.

Passive data collection

The low costs of the citizen-science method were facilitated by shifting the focus away from active to passive data collection by tourists. This approach allowed us to overcome the challenges surrounding user uptake and implementation costs that have traditionally inhibited the capacity to develop sustainable, robust citizen-science monitoring programs (e.g. Steger and Butt, 2015). Specifically, although citizen-science data has been used in studies of species occupancy (Farhadinia et al., 2018), density (Scott et al., 2018), population trends (Strien et al., 2013), and resource use (Broman et al., 2014; Shumba et al., 2018), significant research effort is often still required to collect the data (e.g. Farhadinia et al., 2018; Shumba et al., 2018). In contrast, our passive approach to data collection is well suited for scalable, long-term monitoring for several reasons: (1) no additional tourist training is required for high-quality data output, reflected in the 95% of carnivores that could be individually identified; (2) citizens are required to expend little additional effort to capture data; (3) the start-up costs to implement the monitoring program are low; and (4) little researcher effort is required to collect the data from citizens.

Reasons (1) and (2) likely contributed to all Santawani groups participating in our project and to the maintenance of the Santawani collaboration, neither of which were likely to have been achieved if the project was perceived to detract rather than enhance the tourist experience (Steger et al., 2017). As such, we argue that the perception that significant incentives are required for citizen-scientist participation is not always accurate (Steger and Butt, 2015). Indeed, our results suggest that if the costs of participation are low enough, the knowledge that citizens are contributing to an important cause may be enough to encourage their participation in monitoring (Nov et al., 2014). As such, we suggest a better approach may be to lower the costs of participation through project design rather than attempt to implement reward systems, which may increase project costs and which we suspect are unlikely to appeal to all potential participants. Future studies should thus consider not only their own data requirements but also how best to (1) provide value to users and (2) test their proposition at the lowest possible cost, perhaps in a framework analogous to emerging start-up businesses (Münch et al., 2013; Ries, 2011).

Emerging technology

Shifting the focus from active to passive data-collection and co-opting the existing effort being spent to find charismatic fauna reduced researcher investments in data collection. As such, data-processing became the highest cost to researchers. Emerging technologies, specifically artificial intelligence (AI), machine learning (ML), and centralised global citizen-science databases, offer an opportunity to improve the economies of scale for the citizen-science method even further (Pimm et al., 2015). In the immediate, researcher processing investments could be reduced by connecting with global citizen-scientists through online citizen-science platforms (Hsing et al., 2018; Swanson et al., 2015). Further, citizen-science and ML-hybridised workflows, where there is an initial sorting of data by algorithms and then fine-scale classification by citizens, would provide expedited data processing that would allow mass quantities of data to be processed relatively quickly (Norouzzadeh et al., 2018). Indeed, recent advancements in the fields of ML and AI now mean that species-level identifications, comparable to human-volunteers, are possible, and can save up to 99% of the time required by citizen-scientists (Norouzzadeh et al., 2018). Thus, there currently exists an opportunity to supplement local citizen-science driven data collection, facilitated by stakeholders on the ground (discussed below), with global citizen-science driven data processing, creating end-to-end citizen-driven monitoring programs. Such programs would: (1) streamline data collection and processing, (2) expedite results communication and assessments, and (3) provide public education platforms with engaged communities of contributors – ultimately, providing an opportunity to shift how the public interacts with conservation (Newman et al., 2012).

Further, considerable investment is being made in the application of AI and ML for promoting conservation outcomes (Microsoft, 2018), and significant recent advances have been made in the automated identification of individual identities within species (Berger-Wolf et al., 2017; Crall et al., 2013). This highlights the likelihood of further future reductions in data processing costs. Such innovations will also benefit camera trapping surveys, for which data processing costs were the second-largest investment for researchers. Ultimately, however, for monitoring protocols requiring specialist skills or extensive fieldwork to collect data (e.g. camera trapping, spoor surveys, and call-in stations) their economies of scale are likely to remain a challenge.

The role of wildlife safari operators

We suggest that targeted partnerships with wildlife safari operators could be used to provide the minimal on-site coordination required for citizen-science data collection and, in this way, could be leveraged to scale the collection of tourist photographs over large spatial scales. Data collection workflows could, for example, be incorporated into standard lodge operating procedures followed during tourist visits, e.g. with guests enlisted during welcome orientations and photographs collected on the guest's final evening. Data could then later be transferred to a centralised database for processing and analyses. In this way, engaging commercial organisations to facilitate monitoring programs would not only further reduce the resource burdens of monitoring but would also provide wildlife operators with a low-cost opportunity to: (1) preserve resources essential to their business models; (2) showcase their commitment to conservation; and (3) improve the guest experience. Indeed, as a result of this project, we have already seen similar monitoring programs being voluntarily incorporated into lodge workflows elsewhere in the Okavango Delta, Botswana.

Selective collaborations with specialist operators could also lead to the monitoring of taxa commonly used as biodiversity and habitat quality indicators, e.g. birds (Butler et al., 2012), and to multi-taxa data streams being collected in the same areas. When considered together, these streams could effectively amount to the multi-species approach that is commonly advocated by conservationists today (Burton et al., 2012; Rich et al., 2016; Yoccoz et al., 2001).

Whilst wildlife tourists travelling with experienced animal trackers (e.g. safari guides) would aid the detection of target species, our presented framework is also applicable to self-guided tourists, provided that measures of effort (i.e. GPS tracks) are available and tourist's species-of-interest align with those to be monitored.

Concluding thoughts

The methods most appropriate for the needs of ecologists and wildlife managers will depend on the wider objectives of practitioners and the resources available at their disposal. For projects specifically interested in monitoring full species assemblages (Rich et al., 2016), answering a wide range of ecological questions (Caravaggi et al., 2017), or with a large resource base at their disposal (e.g. Panthera; Rich et al., 2017), the additional costs – time and financial – associated with camera traps may be justified. However, in practice, resources for conservation are often constrained (Leverington et al., 2010; Steger et al., 2017). As such, the performance and cost of the citizen-science method may be best suited to the monitoring needs and resources of many conservationists, provided that wildlife tourism is present within the monitoring areas and that the interests of tourists align with the species to be monitored. The additional information provided by photographs (Swanson et al., 2015), the opportunity to reduce costs further through emerging technologies (e.g. Berger-Wolf et al., 2017; Norouzzadeh et al., 2018), and the potential to shift how the public interacts with conservation (Newman et al., 2012) further advocates the use of the citizen-science method in establishing longitudinal monitoring programs within protected areas with wildlife tourism. Further, the use of tourist photographs to gleam information on population demographics is applicable to a range of taxa, including those commonly used as biodiversity indicators (Butler et al., 2012; Ocampo-Peñuela and Winton, 2017). As such, developing partnerships with wildlife safari operators to coordinate local-level data collection and using global citizen-science platforms (e.g. Zooniverse) to facilitate data processing could lead to sustainable citizen-led monitoring programs that aid the management of protected areas and help to rapidly identify declining populations requiring intervention. This promises to be a challenging but rich opportunity.

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Author contributions

KR conceived the study; KR, CB, and CC collected the data; KR led the analyses with contributions from CB, DM, LR (LR ran camera trap SECR models); KR led the manuscript writing with contributions from CB and LR, specifically in camera trapping, spoor survey, and call-in station method sections; CB, LR, MH contributed to manuscript revisions. JM provided the research infrastructure for field data collection.

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Supplementary material

Table S1: Parameters specified in citizen-science SECR models for each species

	Burn-in	Iterations	Buffer (km)	State Space (km^2)
Lion	5,000	55,000	25	4,760
Spotted hyaena	15,000	150,000	25	4,760
Leopard	1,000	11,000	15	2,400
Wild dog	5,000	55,000	25	4,760
Cheetah	-	-	-	-

Table S2: Parameters specified in camera trap SECR models for each species

	Buffer	State Space (km^2)
Lion	9,000	636
Spotted hyaena	-	-
Leopard	12,000	942
Wild dog	24,000	2,731
Cheetah	-	-

Table S3: Summary of equipment used for different survey methods (bold in items column) and their costs. Fuel costs (per km) are also presented at the bottom of the table.

Item	Description	Total cost
Citizen-science		
i-Got-U GT-120 GPS logger	Used to track tourist movements during game drives. Total cost = unit price: $59.95 * 2	$ 119.90
Camera trapping		
Reconyx® XR6 UltraFire camera trap	Used to capture species images. Total cost = unit price: $599.13 * 13	$ 7,788.69
San Disk Ultra Memory Cards (32 GB)	Used to store camera trap images. Total cost = unit price: $6.99 * 13	$ 90.87
Rechargeable AA batteries and charger	Used to power camera traps (6 required per trap). Total cost is for 120 rechargeable AA batteries ($11.99 for 12 batteries * 10) and $20.00 for a battery charger unit. 120 batteries were required so that half of the camera units could have batteries replaced each camera trapping trip.	$ 139.90
Camera trap poles, brackets and bolts	Used to mount camera traps along roads - were custom made. Total cost is for materials for 13 poles, nuts and brackets ($422.95) and labour costs ($120.84).	$ 543.79
Call-in station		
JBL JRX212 12" speaker	We used the Tannoy CPA 12 speaker left by a previous study. This model has now been discontinued, and so for the total price we present the cost for the JBL JRX212 12" - a speaker with similar specifications.	$ 249.99
BOSS Audio R1100M amplifier	We used the Boss CXX1002 amplifier left by a previous study. This model has now been discontinued, and so for the total price we present the cost for the BOSS Audio R1100M - an amplifier with similar specifications.	$ 44.94
Hotechs MP3 music player and auxiliary cable	Used to play sound files used in call-in station surveys. Total cost = music player price ($19.99) and auxiliary cable price ($4.99).	$ 24.98
Fuel costs	Fuel consumption was estimated as $0.09 per km based on the average fuel consumption of our field vehicle (0.10 litres per km) and average fuel price over the course of the study ($0.86 per litre).	-

Table S4: Definitions of citizen-science SECR model parameters. Table adapted from (Broekhuis and Gopalaswamy, 2016).

Model parameter	**Definition**
N_s	Total number of individuals present within the state space.
σ	Detection probability rate of decline with increasing distance from where an individual was sighted and its activity centre.
β_{sex}	Difference between male and female individuals' complementary log-log detection probability values.
β_{eff}	Rate of change in complimentary log-log detection probability with increased search effort of one unit (here, one unit is equal to one km)
λ_0	Basal encounter rate of an individual whose activity centre is located precisely within the centre of the searched grid cell.
ψ	Ratio: true number of individuals within population/number of individuals within data augmented population
Ψ_{sex}	Proportion of all individuals within the state space that are male.
ϑ	Estimated detection function shape, with values ranging from 0.5 (Exponential shape) to 1 (Gaussian shape)

CHAPTER 6:

General conclusion

The broad aim of this thesis was to enhance our understanding of the relationships between leopards and their competitors. The research presented over the previous four chapters advances our knowledge of the mechanisms facilitating coexistence amongst African large predators and presents a framework for the sustainable monitoring of charismatic fauna within protected areas.

In this chapter, I synthesise the key results of my thesis in the context of coexistence and monitoring within the African large predator guild and discuss the broader contributions and significance of this work. Throughout, I consider the limitations of my work, present solutions, and offer recommendations for further lines of research. The chapter then concludes with a final summary and closing thoughts.

Spatio-temporal partitioning

The work presented in *Chapter two* investigated broad-scale spatio-temporal partitioning between leopards and most other large African predator guild members, complementing previous studies that have primarily focussed on partitioning within the leopard-lion dyad (Balme et al., 2017b; Miller et al., 2018). I found no differences in the volumes of overlap of areas intensively used by leopards with those intensively used by lions, wild dogs and cheetahs, despite the different levels of risk presented by different guild members. I also found no evidence that activity partitioning was driven by predator avoidance. As such, our results suggest that predator avoidance may have a limited role in shaping leopard niches, with resource requirements perhaps instead playing a greater a role, as has been seen in other populations of leopards (Miller et al., 2018) and in other large carnivore species (Broekhuis et al., 2013; Swanson et al., 2016).

Having said this, I acknowledge that my study did not have the data to directly quantify the role of bottom-up forces in shaping leopard space-use. Whilst the inclusion of habitat maps would have allowed the effects of bottom-up forces to be modelled alongside top-down effects when considering spatial distributions, such data was not available at the time of this study. This is important to consider because the strength of top-down within the large predator guild may be shaped by the density of resources and habitat structure. Within Asia, for example, in some ecosystems with low prey densities, leopard and dhole distributions are shaped by tiger avoidance (Steinmetz et al., 2013), whereas in prey rich habitats there is limited evidence of spatial avoidance between the species (Karanth and Sunquist, 2000).

A large African predator guild-wide comparison of fine-scale habitat selection is underway using data provided by this project. Regardless, the results concur with previous studies suggesting that the population-level effects of lions on leopards are minimal (Balme et al., 2017b; Miller et al., 2018) and provide evidence that this relationship is similar between leopards and other guild members.

An additional limitation of our analyses arose due to the data being obtained exclusively from male leopards; however, Miller et al. (2018) and Balme et al. (2017a) found comparable results to ours using data from both sexes, and thus, our results are likely also applicable to females. It is, however, likely that the costs of intraguild encounters change across life-history stages, and so it is conceivable that leopards show increased spatio-temporal partitioning during certain life-history events. Intraguild competitors are, for example, the highest source of leopard cub mortality in some areas (Balme et al., 2013), and so when rearing young, female space use may be heavily influenced by competitor avoidance. My decision to focus exclusively on male leopards was based on relative collar weights to female body mass, i.e. females in the area were ~50% smaller than males (K. Rafiq, unpublished data), and how this impacted the seating of the collar against female leopard necks. This is a problem, however, unlikely to be faced by future studies due to the increasing miniaturisation of telemetry technology (Kays et al., 2015; Wilmers et al., 2015).

Direct intraguild encounters

The results from *Chapter two* raise questions on the implications of high levels of spatio-temporal niche overlap on intraguild encounter onsets and on the fine-scale mechanisms employed by leopards to coexist with competitors. In *Chapter three*, I thus capitalised on the high-resolution nature of my dataset to quantify the occurrence and outcomes of encounters across temporal cycles and broad-scale habitat classifications. In the context of encounter occurrence, the results suggested that high activity overlaps contribute to increased encounters. As such, even in instances where temporal niche partitioning is not driven by predator avoidance (Kronfeld-Schor and Dayan, 2003), shifts along the temporal niche axis could still have implications for competitor dynamics. This is particularly pertinent in an era when anthropogenic disturbances are rapidly shifting the structure and species compositions of some ecosystems (Creel et al., 2018; Dirzo et al., 2014; Malhi et al., 2016), with conceivable knock-on effects on the niche axes of the species that coexist within them. Some species within the large predator guild may be particularly susceptible to these changes because of high reproductive (Durant et al., 2004; Groom et al., 2017) and kleptoparasitism (Carbone et al., 1997) costs inflicted by intraguild competitors, and these species tend to show avoidance behaviours at a fine-scale which reflect the risks of encounters (Broekhuis et al., 2013; Swanson et al., 2016; Webster et al., 2012). However, my results from *Chapter three* suggest that leopard behaviours and movements are minimally impacted during intraguild encounters, with aspects of the leopard's life-history and ecology likely facilitating its coexistence within close-proximity to other guild members (Balme et al., 2017a; Stein et al., 2015).

In *Chapter three*, we did not directly consider the costs incurred by kleptoparasitism because of the difficulties in remotely identifying feeding locations from telemetry data. Although previous studies have used spatial clustering algorithms to identify kill locations (Gese et al., 2016), pilot-studies showed that these methods performed poorly in identifying kill locations within our study area. This may have been a reflection of the difficulties in safely ground-truthing data within the wooded habitats favoured by leopards at the study site or the leopard's propensity to move smaller kills between locations. I do acknowledge, however, that although leopard prey hoisting can significantly reduce the loss of kills, the reproductive success of leopards can still be impacted by high kleptoparasitism rates (Balme et al., 2017a), particularly by spotted hyaenas, and thus, kleptoparasitism is an important consideration of intraguild encounters. Consequently, I and other researchers at the Botswana Predator Conservation Trust (BPCT) are currently collaborating with researchers from the University of Twente, Netherlands, to apply machine learning techniques in the identification of *kill signatures* from fine-scale GPS and accelerometer data collected by the carnivore radio collars used at our study site. An interesting line of future research would thus be to consider the interactions occurring between leopards and their competitors at kill sites and the energetic costs of encounters. Specifically, using the fine-scale data collected by radio collars during periods of high acceleration prior to feeding bouts (presumably hunts) would allow energy expenditure for prey capture to be quantified (Hubel et al., 2016). Considering this alongside remotely identified occurrences of displacements from kill sites would allow us to quantify the energetic limitations placed on leopards by dominant guild members (e.g. Carbone et al., 1997; Gorman et al., 1998). This is important as, even without kleptoparasitism, large carnivore species may already be constrained by energetic requirements (Carbone et al., 2007). Such a study would help to identify the scenarios under which the energetic costs of prey loss may begin to suppress leopard populations and would provide insights into the consequences of increased competition within areas of reduced niche partitioning, e.g. those experiencing prey simplification (Creel et al., 2018).

Intraguild interactions and the mesopredator release framework

From a broader perspective, the results from *Chapters two* and *three* add to a growing number of studies (Broekhuis et al., 2013; Miller et al., 2018; Swanson et al., 2016) suggesting that interactions between large carnivores may not always be well explained within a mesopredator release framework (commonly considered universal across ecosystems and species) (Allen et al., 2017). In particular, considered alongside other studies, my results support the hypothesis that the ecology and life history of leopards can facilitate their coexistence with dominant competitors with few population-level impacts (Balme et al., 2017b; Miller et al., 2018). These results may reflect the fact that: (1) the African large predator guild has remained functionally intact from late-Pleistocene mass extinctions (Dalerum et al., 2009); (2) our study area ecosystem remained relatively intact from human disturbance; and/or (3) our study area had a high and stable prey base (K. Rafiq, unpublished data). For example, studies within Asian predator assemblages have found that spatial and temporal overlaps between competitors are higher in systems with low prey densities (Karanth et al., 2017), perhaps because subordinate predators are forced to co-occupy the same areas as dominants in order to meet resource requirements. As such, my results provide insights into historical coexistence benchmarks amongst large African predators, which could be used as a comparison against fragmented competitor assemblages or competitor populations restricted to patches of shared land with suboptimal resource availability.

Leopard scent marking strategies

In *Chapter four,* I then went on to consider a mechanism thought to be key in facilitating social cohesion and territorial maintenance within felids (Wittmer et al., 2014). Using a long-term behavioural dataset and high-resolution GPS radio collar data, I showed that leopards exhibit a boundary scent marking strategy by increasing marking investments in peripheral areas of their home range and also showed that marking investments increase on roads. As such, these results also suggest that roads may now play a key role in facilitating communication within some leopard populations, presumably by concentrating olfactory information along routes where it is most likely to be encountered. Interestingly, I found that leopard scent marking frequencies in the Okavango Delta were comparable to leopards from similarly productive ecosystems (Jenny, 1996), but were approximately three times higher than leopards from less productive habitats, such as the Kalahari (Bothma, 2004). This suggests that the surrounding environment impacts the optimal scent marking strategies exhibited by leopards and that leopards can be highly flexible in the strategies that they choose. Further, the results within *Chapter four* support the hypothesis that scent marks have a function role in territorial maintenance, with familiarity of neighbours playing a role in the maintenance of stable territories. I acknowledge, however, that spatio-temporal placements are not enough to conclusively assign functions to scent marks (Gosling and

Roberts, 2001), and that for this, additional consideration of scent mark recipients (Allen et al., 2016; Harmsen et al., 2010) and of the olfactory content of scent marks (Soso et al., 2014; Soso and Koziel, 2017) is required. As such, as a continuation of this project's study into leopard olfactory communication, the BPCT will host a PhD candidate investigating the chemical composition and olfactory content of leopard scent marks.

Using tourist photographs for wildlife monitoring

In *Chapter five,* I developed a new framework for estimating wildlife population densities from photographs taken by tourists on safari, which was implemented and tested against traditional monitoring methods. The results were promising. Data for the citizen-science monitoring was the most cost-effective to collect and provided density estimates for a comparable number of species as most of the other tested large carnivore monitoring methods. Promisingly, this was also the method whose costs are most likely to decline with advances in machine learning and artificial intelligence (Cho, 2016; Norouzzadeh et al., 2018). Further, tourist-derived species density estimates with poor accuracy were likely attributable to the small sampling area and limited species sightings. I had limited resources available for collecting citizen-science data because of the need to carry out several monitoring programs simultaneously. Now that the comparison between methods has been made, by focussing on the collection of tourist-derived images from multiple lodges, future projects could overcome these issues and improve estimates across all large predator guild members.

In its current form, this framework will allow safari operators to implement their own large carnivore monitoring programs by leveraging the data being collected by their guests on a daily basis. This would allow basic monitoring infrastructures to be established with relatively low cost and resource requirements. Indeed, as a result of this study and *technical guides* that I have created, one safari operator has already begun implementing the monitoring program at two of their lodges and is showing interest in expanding to a further two lodges in Botswana before the year's end. Systematic monitoring in this way, by a network of safari operators, would provide wildlife managers with the data required for improved monitoring of the country's protected carnivore populations. This is important for Botswana as wildlife tourism is the country's second largest economic sector (World Travel and Tourism Council, 2017), and indeed, increased monitoring is a focal objective for Botswana's Ministry of Environment, Wildlife, and Tourism (Department of Wildlife and National Parks, 2016; Gureja et al., 2014).

More broadly, the approach outlined by this study could be adapted to facilitate the monitoring of other taxa and areas across the globe, with the only pre-requisites being that wildlife tourism occurs within the area and that tourist interests align with the species to be monitored. As such, selective partnerships with a range of niche and non-niche safari operators could effectively lead to multiple streams of data on a wide range of species occupying the same area. Combining this with citizen-science (Swanson et al., 2015) and/or machine learning/artificial intelligence (e.g. Berger-Wolf et al., 2017; Norouzzadeh et al., 2018) image classifications could lead to streamlined data collection and processing work streams. The data provided from such workflows would allow near-continuous, low-cost monitoring of wildlife populations within protected areas.

Further, it is likely that the full potential of the monitoring and conservation applications of the data collected from such workflows is unknown. The development of continuous streams of *big data* on wildlife species may stimulate investment into the development of models and statistical approaches which fully exploit the data being collected. This would be analogous to the growth in camera trapping methods publications that have accompanied the uptake of camera trapping surveys by ecologists in the last two decades (Meek et al., 2015; Rowcliffe et al., 2008).

Conclusion

In summary, my results provide important information on the ecology and monitoring of large African predators and provide insights and tools applicable to other species assemblages. Specifically, I found that the impacts of intraguild competitors on leopards are limited at both a broad- and fine- scale. The results presented suggest that resource acquisition, rather than predator avoidance, may be the primary force driving the spatial and temporal activity patterns of leopards, but I acknowledge that at this stage, this is speculation. I also showed that although high activity overlaps increased encounters between leopards and other guild members, within our study population, leopard behaviours and movements were largely unaffected by encounters. In this respect, habitat structure and the leopard's ecology and life history traits likely contribute to its ability to coexist in such close proximity to its competitors. The work in *Chapter four* then identified that leopards show a boundary scent marking strategy and highlighted the importance of roads in facilitating information transfer between conspecifics. Finally, the monitoring framework detailed in *Chapter five* provided a way to utilise the data being collected by tourists on a daily basis into a wildlife monitoring program. It showed that such programs are low-cost to implement and can provide accurate density estimates for different large carnivore species. Indeed, *technical guides* have been produced as an output of this research and have already been used to implement these monitoring programs elsewhere, with great success, and their continued implementation is expected.

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