From inventories to interactions: inferring mammal community patterns and processes from camera trap data

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by

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Abstract

From inventories to interactions: inferring mammal community patterns and processes from camera trap data.

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The deployment of camera traps, which automatically take pictures of wild animals moving in front of them, is now routinely used to survey terrestrial mammal communities worldwide. The resulting photographic data are used to answer questions relating to the richness and structure of mammal communities, the density of their component species, and how the latter might interact. This thesis fills key methodological gaps in how these questions are addressed. My first data chapter assesses how the exact placement of camera traps on natural game trails influences the characterisation of community richness, composition and structure in an east African savannah landscape. I find that a trail-based placement strategy leads to more species being detected more rapidly relative to a random one, and increases capture rates for carnivore species in particular. In contrast, I reveal in Chapter 3 how a non-random camera trap placement strategy can bias estimates of absolute density for an unmarked large carnivore, the lion

Panthera leo, obtained using an ideal gas model approach. Chapter 4 considers spatiotemporal patterns in camera trap data, and to what extent they can be used to infer on the kleptoparasitic and predatory tendencies of spotted hyenas and lions, respectively, in Tanzania's Ruaha landscape. I find patterns to be generally uninformative, and so, in Chapter 5, turn to another method of collecting spatiotemporal data, Global Positioning Satellite telemetry, to make inferences on the spatial response of elk to wolves in Yellowstone National park. I find no evidence for a significant spatial avoidance of wolves by elk, suggesting that species interactions may not always lead to measurable spatial patterns. Nevertheless, in my final chapter, I use an individual-based modelling framework to simulate different types of prey responses to predator movement in the absence of confounding factors, and find that a huge amount of camera trapping effort would be required to distinguish between them. This thesis highlights how camera trap placement can affect the description of mammal communities and the estimation of species density. It also shows that we cannot rely solely on spatiotemporal patterns derived from camera traps to make inferences on complex interactive processes.

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Chapter 7

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Chapter 1

Introduction

Technology is revolutionising the way we study and monitor all levels of biodiversity (Kays et al. 2015a, Pimm et al. 2015), from solar-powered tracking devices fitted to individual animals, to high resolution satellite images of entire land- and seascapes. Sensors of all kinds are being deployed in habitats ranging from tropical forests to arctic tundra, providing data on the presence and behaviour of numerous species in a way that is far more cost-effective than any other form of survey methodology involving human observers. In particular, the deployment of arrays of remotely triggered camera traps, which automatically take pictures of animals moving in front of them, is now routinely used to survey terrestrial mammal communities all over the world for both conservation and research purposes (Rowcliffe and Carbone 2008, O'Connell et al. 2010, Ahumada et al. 2011, Meek et al. 2014a, Burton et al. 2015).

Modern day camera traps can be described as weatherproof digital cameras equipped with a sensor (motion or infrared), a flash for night-time images (incandescent or infrared), and a data storage unit (Rovero et al. 2013).

They can be adjusted using a wide range of settings, which control the sensitivity of the sensor, the resolution and number of pictures taken at each trigger, and the time delay between consecutive triggers. Camera traps are typically deployed in a grid or transect formation (O’Connell et al. 2010), which is left in place for a period of time that can range from a few days to a number of years (Swanson et al. 2015). During the survey period, images of passing wildlife are taken continuously during the day and at night, with the time of capture being automatically recorded (van Schaik and Griffiths 1996). Thus, at their most basic, photographic data from camera traps consist of standardised records of time, location and species.

The huge appeal of camera trapping lies in the fact that spatiotemporal information is collected non-invasively on a potentially wide set of sympatric species. Consequently, over the past 20 years, camera trap surveys have been used to document the richness and composition of mammal communities in forested environments (Ahumada et al. 2011, McCallum 2013), estimate the relative or absolute abundance of their component species (Carbone et al. 2001, Jenks et al. 2011, Swanson et al. 2015), and, more recently, to make inferences on inter-specific interactions (Linkie and Ridout 2011, Bischof et al. 2014, Gompper et al. 2016). For many of these applications, however, significant biases still arise from both the way camera trapping studies are designed and the inadequacy of current analytical methods used to draw inferences on complex processes involving multiple species. These biases have hindered the adoption of camera trapping as a go-to method in community ecology.

With this in mind, I ask how camera trapping can be optimised to provide a highly versatile, reliable and cost-effective tool for use in the context of mammal community ecology. I do this by addressing biases in the basic design of surveys targeted at multiple species (Chapter 2), testing novel approaches enabling density estimates to be obtained for species that do not lend themselves to capture-recapture analysis (Chapter 3), and developing, as well as testing, approaches to infer the potential for interaction between sympatric species (Chapters 4). Throughout this thesis, I endeavour to adopt a pragmatic point of view, aiming to give a critical account of the extent to which camera traps can realistically be used to characterise community-level patterns and inform on the processes underlying them. In the case of inter-specific interactions, this leads me to test an alternative method, namely Global Positioning Satellite (GPS) telemetry (Chapter 5), and to perform a simulation study in which observed spatiotemporal patterns can be clearly linked to interactive processes (Chapter 6). In the following sections, I provide a brief introduction to each chapter, placing it in the context of previous research and highlighting why the questions addressed are important.

Camera trap placement strategy for multi-species surveys (Chapter 2)

Most simply, camera trapping can be used to document the identity and number of species present within a defined area (Tobler et al. 2008a). Diversity measures such as estimated species richness can be derived from species accumulation curves (Colwell et al. 2004, Tobler et al. 2008a), where the amount of sampling effort obtained by summing the total number of days each camera was active. More recently, occupancy models that account for imperfect detection have been fine-tuned for use in community studies (Dorazio et al. 2006, Rovero et al. 2014) In some instances, camera trap surveys may document species in an area for the first time, and on rare occasions even reveal species that are completely new to science (Rovero et al. 2008). Community-wide surveys can also inform on the structure of a given mammal community, and how it might respond to different types of land-uses (Kauffman et al. 2007a, Kinnaird and O'Brien 2012).

A key notion inherent to multi-species survey methods, be they transect walks, pitfall traps or remote cameras, is that of species-specific detection probability. For any given method, there will be species that are more likely to be recorded as present than others, despite all of them being present in the surveyed area (Mackenzie et al. 2002). In the case of camera traps, a species' detection probability describes the likelihood that it will be photographed if it is present. This likelihood can vary across species, often as a result of a combination of different factors, including density (abundant species are more likely to be photographed, Carbone et al. 2001), body size (smaller species are less likely to activate the camera trap sensor; Anile and Devillard 2015), space use (e.g. camera traps placed on the ground are ill-suited to detecting arboreal species; Oliveira-Santos et al. 2008), camera placement strategy (e.g. exclusive placement on trails will fail to capture those species that never use them; Harmsen et al. 2010, Wearn et al. 2013), habitat type (e.g. some species may actively avoid some types of habitat), and time of survey (e.g. some species may be more or less present in a given area depending on the time of year).

Some of these sources of variation can be minimised by using an appropriate camera trap survey design. For example, camera trap deployment can be stratified across pre-determined habitat classes, thus incorporating potential heterogeneity into the sampling process (Kelly and Holub 2008, Rovero et al. 2013). Surveys may also be repeated at different times of the year to allow for detection of species whose activity varies seasonally (Ikeda et al. 2015), e.g. migratory species. Variation in body size may be tackled by adjusting the height of cameras to ensure detection of the smallest target species (Meek et al. 2014b). Alternatively, analysing the spatial distribution of locations when a species first enters the camera detection zone and triggers the camera has recently been suggested as a post-hoc method of correcting for species body size (Rowcliffe et al. 2011).

In Chapter 2, I assessed how the strategy used to determine the exact location of camera traps to within a few meters (hereafter, placement strategy) can influence inferences made from community-wide surveys of terrestrial mammal species. I compared community-level patterns (richness, composition and structure) from two temporally and spatially concurrent camera trap surveys carried out in Tanzania's Ruaha National Park, which employed different placement strategies, either random or game-trail based. Placement of camera traps on man-made or natural game trails remains the most common strategy in use today when implementing multi-species surveys, despite a number of studies highlighting the differential use of these features by target species in tropical forests (Harmsen et al. 2010, Wearn et al. 2013). In Chapter 2, I carried out the first assessment of the influence of camera trap placement strategy in a savannah landscape. I found that placing cameras exclusively on game trails resulted in more species being described as present, more quickly, and facilitated the detection of rare species during the wet season. Given adequate sampling effort, however, differences in community richness and structure between the two surveys were minimal.

Estimating the density of an unmarked species using an ideal gas model (Chapter 3)

Although the rate at which a species is photographed can provide information on its relative abundance (Carbone et al. 2001), a reliable estimate of absolute abundance or density is often a more valuable (Jennelle et al. 2002, Sollmann et al. 2013). This is especially the case when assessing the status of threatened species (Wang and Macdonald 2009, Alexander et al. 2015, Qi et al. 2015). In particular, absolute measures of animal density can be compared between different geographical areas, as well as over time, and when obtained for multiple sympatric species, can be used to construct more reliable models of community structure.

Camera trap data are well suited to the application of capture-recapture (CR) models to estimate absolute abundance. Such models are based on the recapture of individually recognisable animals of a target species, enabling individual capture and recapture probabilities to be estimated over a specified number of trapping occasions. Population size can be estimated as a parameter in closed CR models, which assume the sampled population is closed to emigration and immigration for the duration of sampling. Capture-recapture models were first applied to camera trap data in the mid-1990s to estimate tiger abundance in Nagarhole National Park, India (Karanth et al. 1995, Karanth and Nichols 1998), and have since provided ecologists with a powerful and versatile framework with which to estimate population size. More recently, a class of spatially explicit capture-recapture (SECR) models has been developed, which allows for information about the capture locations of individuals to be incorporated into the modelling process, thus resulting in an estimate of density rather than abundance (Efford 2004, Borchers and Efford 2008, Royle et al. 2009).

A key pre-requisite to the application of both CR and SECR models is that animals of the target species can be individually recognisable, either by comparing natural markings such as spots or stripes, or by using opportunistic markings visible on camera trap images. Although a number of studies have attempted to apply CR methods to unmarked species by considering markings such as scars, ear-notches or broken horns, these are liable to misidentification, which in turn can heavily bias density estimates (Foster and Harmsen 2012). Kelly et al. (2008) found that misidentification errors across different observers could bias density estimates by over 100%. Indeed, relatively few species are individually recognisable, and as a result, the majority of camera-trap studies aimed at estimating species density have been focused on spotted or striped felids (O'Connell et al. 2010). Somewhat paradoxically, few well-established analytical methods exist for estimating densities of unmarked species (although see Chandler and Royle 2013), despite these representing the majority of species likely to be caught on camera traps (Rowcliffe et al. 2008, Tobler et al. 2008b, Ahumada et al. 2011).

In Chapter 3, I tested the applicability of a relatively new method of density estimation, the random encounter model (REM), which uses the rate of contact between moving animals and static camera traps to estimate animal density (Rowcliffe et al. 2008). The model assumes that individual animals encounter camera traps in the same way that randomly moving particles encounter one another in an ideal gas (Hutchinson and Waser 2007). This requires that camera traps be placed randomly with respect to animal movement (Rowcliffe et al. 2013), an assumption that has proved challenging to satisfy in practice (Foster and Harmsen 2012). Using data from an extensive array of cameras deployed in Serengeti National Park, Tanzania, I assessed whether the REM can be used to estimate the density of an unmarked and threatened large carnivore, the lion (*Panthera leo*).

Inferring species interactions in an African mammal community (Chapter 4)

While Chapters 2 and 3 of this thesis contribute towards improving the way in which we describe mammal communities using data from camera trap surveys, the remaining chapters investigate to what extent we can characterise some of the underlying interactive processes that structure communities. Inter-specific interactions are notoriously difficult to characterise in the wild, with most interactive behaviours being either too infrequent (e.g. predators hunting prey, antagonistic encounters between members of the same guild), or too subtle (e.g. avoidance behaviours, olfactory signals) to be studied through simple observation. Moreover, mammal species generally occur at low densities and in environments that tend to preclude day-to-day observation. Alternative field-based methods, such as diet analyses from scat samples (Klare et al. 2011) or exclusion/removal experiments (Grant 1972, Terborgh et al. 2001, Du Preez et al. 2015), are logistically demanding and generally not feasible in the case of rare or protected species (Davison et al. 2002, Piggott and Taylor 2003, Long et al. 2012).

Given these challenges, researchers are increasingly resorting to the use of spatiotemporal data to make inferences on how species interact (Potts et al. 2014). In particular, a growing body of literature has developed around the notion that quantifying the likelihood that two or more species co-occur in space and/or time may offer insights into whether they are likely to interact or not (Mackenzie et al. 2004, Waddle et al. 2010, Veech 2013). In the case of camera trapping, this realisation has led to the development of a range of methods aimed at comparing patterns in the timing and location of photographic captures across sympatric species. The resulting approaches can be broadly categorised into two types: those that consider co-occurrence in either dimension (time or space) by aggregating observations in the other (i.e. static measures of interaction), and those that consider both dimensions simultaneously (i.e. dynamic measures of interaction) (Benhamou et al. 2014).

Static measures of interaction consider the extent to which the spatial and temporal habits of two species overlap. Strictly spatial approaches assess the absolute or relative use of camera trap locations by each species over an extended period of time (usually the entire study period), and investigate whether or not these are correlated. This approach has been implemented in various forms, from simple count models through to more complex occupancy models that account for imperfect detection (Mackenzie et al. 2004, Waddle et al. 2010). In contrast, strictly temporal approaches focus primarily on the timing of photographic events within the 24-hour cycle, which can be used to construct species-specific activity patterns (Van Schaik and Griffiths 1996, Rowcliffe et al. 2014). The latter can be compared across species and a measure of temporal overlap estimated from them (Ridout and Linkie 2009, Linkie and Ridout 2011).

The relative value of static approaches is likely to be dependent on the nature of the interaction under investigation. For instance, interference competition between sympatric carnivores may be mitigated by a segregation of activity in space (the two species use different areas; e.g. Kays et al. 2015b) or in time (one species may become more nocturnal and the other diurnal; Bischof et al. 2014). In this case, segregation in only one of these dimensions permits coexistence. Characterising either spatial or temporal segregation has been the focus of numerous studies in recent years, most of them focusing on intra-guild competition in medium to large carnivores, for which avoidance behaviour is expected (Schuette et al. 2013, Bischof et al. 2014, Lesmeister et al. 2015, Sunarto et al. 2015). In contrast, interactive behaviour involving a degree of proximity between individuals of two different species, such as predation and parasitism, can only be characterised by considering space and time simultaneously. Indeed, two species may overlap completely in their spatial and temporal habits (i.e. a high level of static interaction in both space and time), yet never use the same site at the same time, and so never encounter one another. Thus, dynamic measures of interaction, which consider whether two species are ever in the same place at the same time, are required.

Chapter 4 describes my attempts to characterise the known kleptoparasitic and predatory tendencies of spotted hyaenas (*Crocuta crocuta*) and lions (*Panthera leo*), respectively, from camera trap data collected in Tanzania's Ruaha National Park. I applied four different methods of quantifying spatiotemporal associations, including two static (activity pattern overlap and co-occupancy modelling) and two dynamic approaches (co-detection modelling and temporal spacing at shared camera trap sites). I found that dynamic approaches offer more promise when characterising the kleptoparasitic behaviour of spotted hyenas with regards to lions than more conventional static approaches. In contrast, observed spatiotemporal associations between lions and the different herbivore species I considered provided no convincing indication of any predatory tendencies. I suggest that the latter finding may not be so surprising given that predator-prey spatiotemporal associations are not only the result of predators seeking prey, but of prey avoiding predators. The latter, opposing process may ultimately result in a much weaker spatiotemporal association being observed between predator and prey.

A closer look at the predator-prey spatial game (Chapter 5)

To gain a better understanding of the spatial patterns that might arise from predator-prey interactions, I turned to the well-studied grey wolf (*Canis lupus*) and elk (*Cervus elaphus*) populations of Yellowstone National Park (YNP) in Northern U.S.A. Wolves were reintroduced to YNP in the mid-1990s following an absence of 70 years in an attempt to re-establish a top down control of thriving elk populations (Mech 1970). What followed constitutes one of the most cited examples of trophic cascades, with wolf predation negatively affecting elk numbers and behaviour, and indirectly contributing to the recovery of over-browsed aspen stands (Ripple et al. 2001, Kauffman et al. 2010, Ripple and Beschta 2012, Painter et al. 2015). In this context, assessing the spatial responses of elk to the movement of wolves has become an extremely active area of research.

Although elk are the primary prey of wolves in YNP, constituting up to 92% of kills during the winter months (Smith et al. 2004), there is still some debate as to whether elk display measurable spatial responses to the distribution and movement of their cursorial predator. Past studies have primarily focused on vigilance levels and fine-scale switches in habitat type as a response to predation risk (Creel et al. 2005, Fortin et al. 2005, Creel et al. 2008), which are commonly framed within the popular "landscape of fear" concept (Laundré et al. 2001, Kauffman et al. 2007b). Few, however, have assessed whether elk proactively avoid areas that are heavily used by wolves (i.e. actively minimise spatial overlap), or react to wolves at a finer spatial scale (i.e. minimise encounter events). This is the question I addressed in

Chapter 5 using Global Positioning Satellite (GPS) collar data collected simultaneously on wolves and elk in YNP’s Northern Range.

Animal-borne technologies, such as GPS collars, provide highly detailed information on animal movements, which has been used as a basis to model habitat use by individuals and populations, to study migrations (Thirgood et al. 2004, Lendrum et al. 2013), to analyse the behaviour of animals in human-dominated landscapes (Hebblewhite and Merrill 2008, Valeix et al. 2009, Oriol-Cotterill et al. 2015), and to gain insights into inter and intra-specific interactions (Merrill et al. 2010, Broekhuis et al. 2013, Courbin et al. 2015). The latter is often carried out by estimating measures of spatial overlap and encounter rate between individuals, which respectively quantify the level of joint space use and the degree to which trajectories “meet” one another over time (Long et al. 2014). Importantly, these measures are analogous to the indices of static and dynamic interaction introduced in Chapter 4 to analyse camera trap data.

In Chapter 5, I estimated spatial overlap and encounter rates between GPS-collared elk and wolves, and tested whether these are significantly lower than expectations based on a null model approach. Following the work of Richard et al. (2013), I generated alternative elk trajectories using three distinct null model formulations, recalculating spatial overlap and encounter rate with the original wolf distribution and trajectories, respectively, to obtain a distribution of expected values. Although common in community ecology (Gotelli & Graves 1996), the null model approach has never been used to investigate the potential for spatial interaction between predators and prey from telemetry data. I revealed an absence of patterns reflecting significant avoidance behaviour for the majority of the individual elk considered. I discuss the possible ecological and methodological reasons underlying this finding.

Inferring prey responses to predators from camera traps: a simulation study (Chapter 6)

Chapters 4 and 5 serve to highlight the fact that spatiotemporal patterns obtained from camera traps or GPS collars often arise as a result of a combination of ecological (e.g. interactions, habitat-use, heterogeneity in species density; Gompper et al. 2016) and methodological (e.g. sampling effort, site/individual selection) processes. Successfully controlling for confounding factors is often challenging, and particularly so when attempting to characterise processes involving multiple species. In particular, this hinders reliable evaluation of the potential for either method to characterise various aspects of species interactions.

In the case of camera trapping, a fundamental limitation lies in the fact that surveys sample only a very small fraction of any given study area. This is because the surveyed area is usually much larger than the field of view of a camera trap. According to Wearn et al. (2013), "2 km^2 grid squares are often used (e.g. Ahumada et al. 2011) compared to sensors with maximum detection zones mostly less than 2×10^{-4} km^2 (Meek et al. 2012)", resulting in 0.01% of the study area being surveyed. An important consequence of this is that the resolution of the spatial data obtained for each species will be coarse, and it can be expected that a high level of sampling effort will be required in order to reliably characterise patterns arising from inter-specific interactions. In Chapter 6, I used a simulation approach to test whether camera trap surveys of varying efforts could be used to discriminate between different spatial responses of prey to the movement of predators.

More specifically, I simulated camera trapping data arising from the sampling of interacting wolf and elk populations in YNP's Northern Range (NR). I employed an individual-based modelling approach to generate elk trajectories that responded to those of wolves according to three distinct avoidance scenarios (or strategies; these terms are used interchangeably hereafter). The first of these, the risky places hypothesis, conceptualised elk as navigating through a heterogeneous landscape of predation risk (Laundré et al. 2001, Laundré 2010). This was a purely spatial response involving proactive, rather than reactive avoidance (Kauffman et al. 2007b). The second saw individual elk responding reactively to the presence of wolves in their immediate surroundings (the risky times hypothesis; Proffitt et al. 2009, Rogala et al. 2011, Middleton et al 2013, Basille et al. 2015, Courbin et al. 2015). Finally, the third scenario followed the risk allocation hypothesis, which states that elk should display less pronounced reactive movement behaviour to the immediate presence of wolves in areas where the latter are often encountered (Creel et al. 2008). I then simulated the deployment of camera trap arrays of varying density (i.e. varying effort) across the NR, and assessed whether each strategy could be distinguished from the resulting spatiotemporal patterns.

Concluding remarks

This thesis is presented as a collection of manuscripts, each with their own supporting information and list of references. Although the first two data chapters have been published in peer-reviewed journals, they have been reformatted here to provide consistency with the other three. In all cases, figures and tables are embedded in the text to facilitate their referral by the reader. Chapters 1 (Introduction) and 7 (Discussion) have a joint list of reference that can be found at the end of the thesis. Finally, I have included one paper as an appendix on which I am co-author. It documents the use of camera trap surveys to assess the co-occurrence of carnivore species in China's Qilianshan National Nature Reserve, and is a fitting example of how this survey methodology can inform potential conservation measures targeted at multiple species.

Chapter 2

Random versus game trail-based camera trap placement strategy for monitoring terrestrial mammal communities

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ABSTRACT

Camera trap surveys exclusively targeting features of the landscape that increase the probability of photographing one or several focal species are commonly used to draw inferences on the richness, composition and structure of entire mammal communities. These studies ignore expected biases in species detection arising from sampling only a limited set of potential habitat features. In this study, we test the influence of camera trap placement strategy on community-level inferences by carrying out two spatially and temporally concurrent surveys of medium to large terrestrial mammal species within Tanzania's Ruaha National Park, employing either strictly game trail-based or strictly random camera placements. We compared the richness, composition and structure of the two observed communities, and evaluated what makes a species significantly more likely to be caught at trail placements. Observed communities differed marginally in their richness and composition, although differences were more noticeable during the wet season and for low levels of sampling effort. Lognormal models provided the best fit to rank abundance distributions describing the structure of all observed communities, regardless of survey type or season. Despite this, carnivore species were more likely to be detected at trail placements relative to random ones during the dry season, as were larger bodied species during the wet season. Our findings suggest that, given adequate sampling effort (> 1400 camera trap nights), placement strategy is unlikely to affect community-level inferences. However, surveys should consider more carefully their choice of placement strategy when targeting specific taxonomic or trophic groups.

INTRODUCTION

Camera trap surveys are used worldwide to inventory and monitor terrestrial mammal communities (Tobler et al. 2008, Ahumada et al. 2011, Rovero et al. 2014). Common outputs from these studies include an assessment of the number of species present (community richness), their identity (community composition) and the distribution of their absolute or relative abundances (community structure), all of which may be used to guide conservation actions (Ahumada et al. 2013). As with most sampling methods that only survey a small fraction of often vast and heterogeneous landscapes (Jones 2011, Meek et al. 2012), choice of an appropriate camera trap survey design is key to obtaining unbiased estimates of these measures (O'Connell et al. 2010, Rovero et al. 2013), especially when space use is highly variable across species (Harmsen et al. 2010). In particular, the strategy used to determine the exact location of cameras down to a few meters (hereafter, placement strategy) can have a considerable influence on species detection probability (Wearn et al. 2013), thereby affecting inferences made at the community level.

Non-baited camera trap placement strategies can be broadly classified into two types (Meek et al. 2014). Non-random placements target features of the landscape – such as game trails, roads, water points and salt licks – that increase the probability of photographing one or several target species. These are typically used in the context of mark-recapture (Karanth et al. 1995, Gopalaswamy et al. 2012) and occupancy (MacKenzie et al. 2002, Sollmann et al. 2011, 2012) studies directed at rare or elusive species. Survey designs in which the approximate location of camera traps across the landscape are chosen randomly, but where exact camera placement is determined by specific features of those locations (e.g. game trails), also fall into this category (Ahumada et al. 2011, Rovero et al. 2014). In contrast, random camera placements are determined a priori by precise geographical coordinates and ignore nearby features that may increase capture probability, meaning that such features are sampled in proportion to their occurrence in the landscape (Rowcliffe et al. 2013). In theory, not only should such randomisation allow a wider variety of landscape features to be sampled, but it should also avoid sampling bias when assessing the presence or relative abundance of multiple sympatric species, particularly when the latter show contrasting space use patterns.

In practice, however, non-random camera placements are still commonly used to draw inferences on the richness, composition and structure of mammal communities, regardless of potential biases arising from sampling only a limited set of habitat features (Srbek-Araujo and Chiarello 2005, Tobler et al. 2008, Can and Togan 2009, Ahumada et al. 2011, Mugerwa et al. 2012, Rovero et al. 2014). Recent studies have highlighted how the use of game trails (i.e. paths created by animals – hereafter, trails), in particular, can vary across species (Kays et al. 2009, 2011), and how this may affect camera trap survey design (Harmsen et al. 2010). For instance, using strictly random camera placements defined as locations within 5 m of a pre-determined GPS point, Wearn et al. (2013) recently obtained a significantly higher detection probability for the endangered and poorly known Bornean bay cat (*Pardofelis badia*) relative to previous camera trap studies that used strictly non-random placements. In the Neotropics, Di Bitetti et al. (2014) and Blake and Mosquera (2014) reached contrasting conclusions on the influence of trail and off-trail sampling in the context of mammal community surveys. Although these studies provide interesting insights into animal space use, they are of limited use to camera trap survey design since a strategy of placing cameras exclusively off-trails is extremely rare in practice.

With the proliferation of large-scale camera trap studies that aim to make inferences at the community level, it has now become important to quantify potential biases arising from the use of non-random camera placements. Past assessments carried out in tropical forest habitats have tended to compare random and trail-based placements that were in different spatial locations, thereby introducing the possibility that the observed differences could have been due to habitat heterogeneity (Harmsen et al. 2010, Wearn et al. 2013). Here, we implement a paired design to survey medium to large terrestrial mammal species within Tanzania’s Ruaha National Park, with strictly game trail-based and strictly random camera placements located within 50 m of each other. We first assess whether the observed communities differ in richness and composition. We then compare the structure of observed communities in terms of their rank abundance distributions (RADs). Finally, we evaluate what makes a species significantly more likely to be caught at trail placements.

METHODS

Ethics statement

Data collection was based on the use of remotely set camera traps, a non-invasive method that does not involve contact with the study species, nor interfere with their natural behaviour. Fieldwork was carried out under research permit no. 2013-285-NA-2013-105 to JJC, issued by the Tanzanian Commission for Research and Technology (COSTECH).

Study area

The study area is situated on the eastern side of Ruaha National Park (RNP) in southern Tanzania between 7°35′ - 7°42′ S and 34°50′ - 34°59′ E (Figure 2.1). RNP is Tanzania's largest National Park, encompassing an area of 20 226 km^2, and supports a diverse community of mammal species, including a full guild of large carnivores (Abade et al. 2014). In contrast to protected areas in northern Tanzania, the Ruaha ecosystem remains largely unstudied. Roads and tourist facilities are concentrated around the Great Ruaha River, which runs along the south-eastern boundary of the Park. Our study focuses on an area of approximately 100 km^2 situated close to the Park headquarters (Figure 2.1).

The climate of RNP is semi-arid to arid, with rainfall peaks occurring from December to January and March to April, and an average annual rainfall of 500 mm (Walsh 2000). Altitude across the landscape ranges from 696 to 2171 m asl. The vegetation cover is a mosaic of typical East African semi-arid savannah and northerly Zambesian miombo woodland, including *Acacia*, *Combretum* and *Comniphora* species (Stolberger 2012). The Great Ruaha River is the main water supply in the study area, providing a key resource for most wildlife during the dry season from June to November.

Camera trap surveys

The study area was first divided into 2-km^2 grid cells in Quantum GIS (QGIS Development Team 2013). Fifty-four adjacent cells were then selected based on ease of access in the field to make up a continuous camera trap array (Figure 2.1). The location of the random camera placement within each cell was chosen randomly and located in the field using a handheld GPS device (Garmin Etrex 10, Garmin International, Inc., Olathe, Kansas, USA). Placement was on the closest tree within a radius of 5 m (or pole if no tree was present) and oriented so as to offer a reasonably uncluttered view. We then identified a clear, natural game trail within a maximum of 50 m of the random placement on which to position the trail-based camera. For the purpose of this study, we defined game trails as continuous, grassless routes through the habitat measuring at least 1 m in width and showing clear evidence of current usage by wild animals (e.g. presence of fresh droppings, spoor, or recently flattened grass either side of the trail). Taken together, the random and trail-based cameras within a given cell formed a sampling pair. It is important to note that, whereas trail-based cameras could never be placed off-trail, random cameras could be placed on a trail if the latter occurred within the 5 m radius defined above. In our case, 16.7% of the random cameras were positioned on trails.

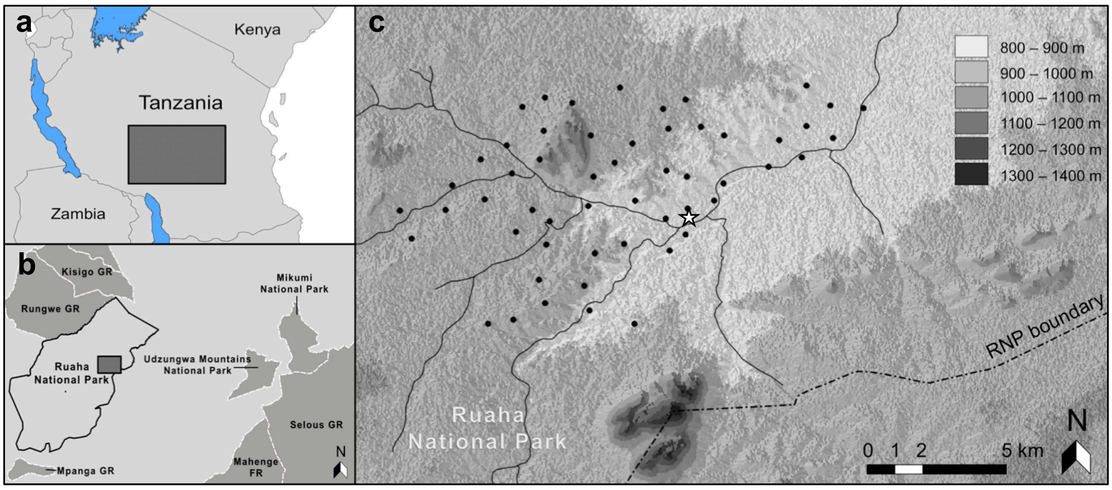

Figure 2.1. Location of random camera placements within Ruaha National Park, southern Tanzania. Insets (a) and (b) show the location of Ruaha National Park (RNP) in Southern Tanzania and that of the study area on the eastern side of RNP. In (c), solid black lines symbolise the river system present around the study area and the white star marks the location of RNP headquarters. Trail-based camera placements were chosen within 50 m of the random placements (back dots).

We took appropriate steps to ensure that no factors other than placement strategy could influence the detection or non-detection of a species. Both cameras within a sampling pair were of the same model (Reconyx HC500, Reconyx, Inc., Holmen, Wisconsin, USA), used the same SD cards (SanDisk 8 GB class 10, SanDisk, Milpitas, California, USA), and all cameras were placed on trees or poles at a height of 0.3 m off the ground. Trail-based cameras were positioned between 3 and 5 meters away from, and at an angle to, the trail to ensure adequate detection of faster moving animals. All cameras were set to take five successive photos per trigger with no delay between consecutive triggers. Date and time were automatically stamped onto each image. Vegetation was cleared for a few meters in front of each camera but not otherwise disturbed. Altitude across camera locations was recorded using a handheld GPS device and ranged from 801 to 956 m (mean = 965.2 m, SD = 40.2 m). The relatively short spacing between paired cameras (≤ 50 m) ensured they sampled the same habitat type.

Sampling periods consisted of 8 successive weeks in both the dry (19th September 2013 – 18th November 2013) and wet season (21st December 2013 – 21st February 2014). Cameras were checked once after four weeks of sampling to change batteries and download memory cards.

Data analysis

Photographed animals were identified down to species level using published guides (Kingdon 2013). Photographic events of the same species were judged to be temporally independent if they were separated by more than one hour (O'Brien et al. 2003). For each camera location (random and trail-based), we computed species-specific relative abundance indices (RAIs) as the number of independent events divided by the number of days the camera was active, and multiplied by 100 (i.e. events per 100 camera trap days; Carbone et al. 2001, Rovero and Marshall 2009). RAIs were also calculated at the survey-level by considering the sum of all events and camera days across a particular survey. Our analyses consider medium to large terrestrial mammals weighing more than 0.5 kg.

Sample-based species accumulation curves were compared using 95% confidence intervals drawn from 200 randomisations performed with replacement. We followed the method of Colwell et al. (2004) and computed confidence intervals based on the unconditional variance. For both seasons, curves were compared at the value denoting the lowest effort between the two types of survey (Chao et al. 2014). We used the Jaccard dissimilarity index (Jaccard 1912) to quantify compositional differences between the observed communities. To compare community structure, we only considered species that were detected in both surveys and whose number of independent events recorded overall was equal or greater than an arbitrary value of five. We fitted null, pre-emption, lognormal, Zipf and Zipf-Mandelbrot models to rank abundance distributions (see Wilson 1991 for details) constructed from the survey-level RAIs of selected species. Model selection was based on the deviance criterion defined as the minimisation of sum of squares of deviations from predicted and observed values (Collins et al. 2008). Although the fitting of models to RADs is an intuitive way of representing and comparing community structures, it does not in itself provide information on the relative rank each species occupies within the observed communities (i.e. rank shifts). In order to assess the latter, we calculated the mean absolute rank shift (MARS) from the random to the trail-based survey using the following formula (see Collins et al. 2008, equation 1):

$$\text{MARS} = \sum_{i=1}^{n} (|R_{i,trail} - R_{i,random}|)/n$$

where n is the number of species considered, and R_i is the relative rank of species i on *random* and *trail*-based surveys. We tested the hypothesis that the MARS was not significantly different from zero using a Wilcoxon signed rank test.

For the same reduced set of species, we also compared RAIs obtained at random and trail-based placements using pairwise Wilcoxon signed rank tests. The latter tested the null hypothesis that the distribution of pairwise differences (trapping rates at random placements minus those at trail placements) was symmetric about zero. The mean of the resulting normal distribution – termed the location shift – and the associated 95% confidence intervals were used to assess the level of significance ($\alpha = 0.05$) relative to zero. Species for which the RAI at trail placements was found to be significantly higher than that at random placements were given a score of 1 whilst others were given a score of 0. We modelled the resulting binary variable as a function of trophic category (carnivore, herbivore, insectivore and omnivore – classification based on Kissling et al. 2014), log body mass (taken from Smith et al. 2003) and social behaviour (solitary/social) using a generalised linear model with binomial errors and a logit link function (Table S2.1). We also considered the interaction between trophic category and log body mass. Model selection was carried out using Akaike's Information Criteria (AIC; Akaike 1974), with subsequent inferences based on the model with the lowest AIC value (Burnham and Anderson 2002).

All analyses were carried out in R version 3.0.3 (R Development Core Team 2013). Species accumulation curves were plotted using the package iNEXT (Hsieh et al. 2013) and analyses of community composition and structure were carried out in package vegan (Oksanen et al. 2013).

RESULTS

Comparison of community richness, composition and structure

Overall, we detected a total of 41 medium-to-large terrestrial mammal species from 10 567 camera-trap days accumulated across seasons and survey types (Table 2.1). The number of false triggers was high for both types of survey, representing 45.1% and 42.6% of all triggers taken by the random and trail-based surveys. False triggers were associated with camera locations in grassland areas, where the increased occurrence of swaying grass caused cameras to trigger even in the absence of any animal. The smallest species we consider in our analysis is the slender mongoose (*Herpestes sanguinea* – 0.6 kg on average) and the largest, the African elephant (*Loxodonta africana* – 3940 kg). Human activities were recorded once at two trail-based camera locations (off-roading vehicles).

We compared sample-based species accumulation curves at sampling efforts of 2820 and 2347 camera trap days in the dry and wet season, respectively (Figure 2.2). Observed species richness did not differ between the two survey types during the dry season (S_{obs} = 38 in both cases). However, a minimum of 650 camera trap days was required to obtain communities that did not differ significantly in their richness. The trail placement survey detected more species during the wet season (S_{obs} = 39) than the random placement survey (S_{obs} = 34), although confidence intervals overlapped marginally at the point of comparison. In contrast to the dry season, at least 1358 camera trap days were required during the wet season to obtain communities that were not significantly different in their richness. In both seasons, the trail-based placement survey reached higher community richness for lower levels of sampling effort (Figure 2.2).

Compositional dissimilarity between observed communities was greatest during the wet season when 17.5%* of the species detected overall were detected by only one of the surveys. During the dry season, communities were more similar, with only 10.0%* of the species being detected by only one survey type. Importantly, community dissimilarity was primarily due to the detection/non-detection of relatively rare (e.g. the African wild dog and the ground pangolin) or habitat-specific species (e.g. the Klipspringer) (Table 2.1).

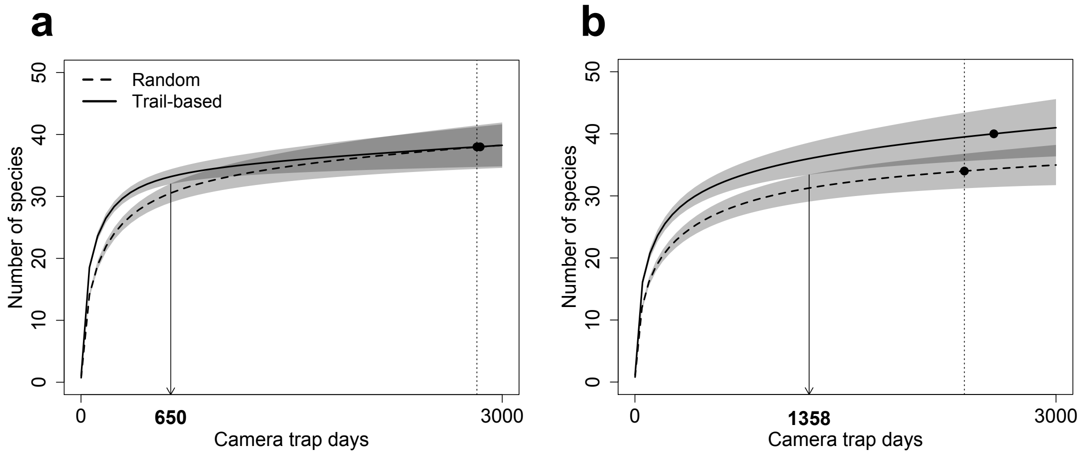

Figure 2.2. Sample-based species accumulation curves describing the medium to large mammal community richness in the study area during the (a) dry and (b) wet season. Shaded polygons denote the 95% confidence intervals drawn from 200 randomisations performed with replacement and based on the unconditional variance. Confidence interval overlap is shown in a darker shade of grey. For each season, curves were compared at sampling efforts symbolised by the dotted vertical lines. Downward pointing arrows and bold numbers on the x-axis mark the level of effort at which the richness of observed communities could not be considered as significantly different.

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* These values represent corrigenda to the ones presented in Cusack et al. (2015)

Table 2.1. List of medium to large terrestrial mammal species (> 0.5 kg) camera trapped in Ruaha National Park, Tanzania**.** The number of independent photographic events and the survey-level relative abundance index (RAI) are given for each season (dry and wet) and type of survey (random versus trail-based placement).

			Independent events				Survey-level RAI			
			Dry season		Wet season		Dry season		Wet season	
Taxonomic group	Latin name	Common name	Rand.	Trail	Rand.	Trail	Rand.	Trail	Rand.	Trail
Primata	*Cercopithecus pygerythrus*	Vervet monkey	9	14	8	17	0.32	0.50	0.34	0.66
	Papio cynocephalus	Yellow baboon	95	120	67	102	3.34	4.26	2.85	3.99
Carnivora	*Canis mesomelas*	Black-backed jackal	44	133	30	65	1.55	4.72	1.28	2.54
	Octocyon megalotis	Bat-eared fox	44	28	26	15	1.55	0.99	1.11	0.59
	Lycaon pictus	African wild dog	-	-	-	2	0.00	0.00	0.00	0.08
	Mellivora capensis	Honey badger	3	9	5	4	0.11	0.32	0.21	0.16
	Mungos mungo	Banded mongoose	3	19	4	7	0.11	0.67	0.17	0.27
	Bdeogale crassicauda	Bushy-tailed mongoose	2	2	-	1	0.07	0.07	0.00	0.04
	Herpestes sanguinea	Slender mongoose	9	15	2	7	0.32	0.53	0.09	0.27
	Ichneumia albicauda	White-tailed mongoose	35	59	11	26	1.23	2.09	0.47	1.02
	Crocuta crocuta	Spotted hyena	99	211	62	165	3.48	7.48	2.64	6.45
	Proteles cristata	Aardwolf	19	78	28	48	0.67	2.77	1.19	1.88
	Genetta genetta	Common genet	18	60	15	26	0.63	2.13	0.64	1.02
	Genetta tigrina	Blotched genet	1	-	-	4	0.04	0.00	0.00	0.16
	Civettictis civetta	African civet	15	35	4	11	0.53	1.24	0.17	0.43
	Felis sylvestris	Wild cat	2	24	6	2	0.07	0.85	0.26	0.08
	Felis serval	Serval	4	21	17	18	0.14	0.74	0.72	0.70
	Felis caracal	Caracal	1	1	-	2	0.04	0.04	0.00	0.08
	Acinonyx jubatus	Cheetah	-	2	2	1	0.00	0.07	0.09	0.04
	Panthera pardus	Leopard	12	54	10	36	0.42	1.91	0.43	1.41
	Panthera leo	Lion	12	44	8	40	0.42	1.56	0.34	1.56

Table 2.1 (cont.)

Pholidota	*Smutsia temminckii*	Ground pangolin	1	-	1	-	0.04	0.00	0.04	0.00
Rodentia	*Hystrix cristata*	Crested porcupine	1	23	3	20	0.04	0.82	0.13	0.78
Ungulata	*Orycteropus afer*	Aardvark	13	13	5	13	0.46	0.46	0.21	0.51
	Loxodonta africana	African elephant	354	428	1146	1671	12.45	15.18	48.83	65.35
	Equus quagga	Common zebra	162	172	144	168	5.70	6.10	6.14	6.57
	Hippopotamus amphibious	Hippopotamus	42	123	66	201	1.48	4.36	2.81	7.86
	Potamochoerus larvatus	Bush pig	1	3	-	4	0.04	0.11	0.00	0.16
	Phacochoerus africanus	Warthog	34	36	68	84	1.20	1.28	2.90	3.29
	Giraffa camelopardalis	Giraffe	229	390	110	165	8.05	13.83	4.69	6.45
	Syncerus caffer	African buffalo	10	12	-	-	0.35	0.43	0.00	0.00
	Tragelaphus scriptus	Bushbuck	6	5	1	1	0.21	0.18	0.04	0.04
	Tragelaphus imberbis	Lesser kudu	20	25	44	28	0.70	0.89	1.87	1.10
	Tragelaphus strepsiceros	Greater kudu	170	215	88	112	5.98	7.62	3.75	4.38
	Taurotragus oryx	Eland	4	3	5	9	0.14	0.11	0.21	0.35
	Sylvicapra grimmia	Bush duiker	60	41	14	36	2.11	1.45	0.60	1.41
	Oreotragus oreotragus	Klipspringer	-	2	-	1	0.00	0.07	0.00	0.04
	Madoqua kirkii	Kirk's dikdik	52	139	69	146	1.83	4.93	2.94	5.71
	Gazella granti	Grant's gazelle	1	1	5	4	0.04	0.04	0.21	0.16
	Aepyceros melampus	Impala	1173	1929	996	1103	41.26	68.40	42.44	43.14
	Kobus ellipsiprymnus	Waterbuck	22	23	3	6	0.77	0.82	0.13	0.23

Thirty species were considered in the analysis of community structure, including 9 carnivores, 12 herbivores, 4 insectivores and 5 omnivores. Based on the deviance criteria, the lognormal distribution provided the best fit for observed RADs resulting from both types of survey as well as for both seasons (Table 2.2; Figure 2.3), thus indicating similar overall community structures. Despite these similarities in overall community structure, the MARS for both seasons was significantly different from 0 (Dry: $V = 351$, $N = 30$, $P < 0.001$; Wet: $V = 253$, $N = 30$, $P < 0.001$), indicating that species occupied different ranks within the observed communities.

Table 2.2. Deviance criteria for the five types of model fitted to rank abundance distributions. The deviance criterion is defined as the minimisation of sum of squares of deviations from predicted and observed values.

Placement	Season	Deviance criterion by model				
		Null	Pre-emption	Lognormal	Zipf	Zipf-Mandelbrot
Random	Dry	23.8	4.9	1.1	8.0	4.6
	Wet	38.6	7.1	3.4	7.4	4.2
Trail	Dry	14.2	6.8	2.2	5.2	4.2
	Wet	23.2	6.2	2.3	4.4	2.8

Species-level determinants of trail use

In both the dry and the wet season, no species exhibited significantly higher RAIs at random camera placements relative to trail-based ones (Table S2.1; Tables S2.2 and S2.3). We therefore only assessed the determinants of species being caught significantly more often at trail placements, which numbered 16 and 12 out of 30 during the dry and wet season, respectively.

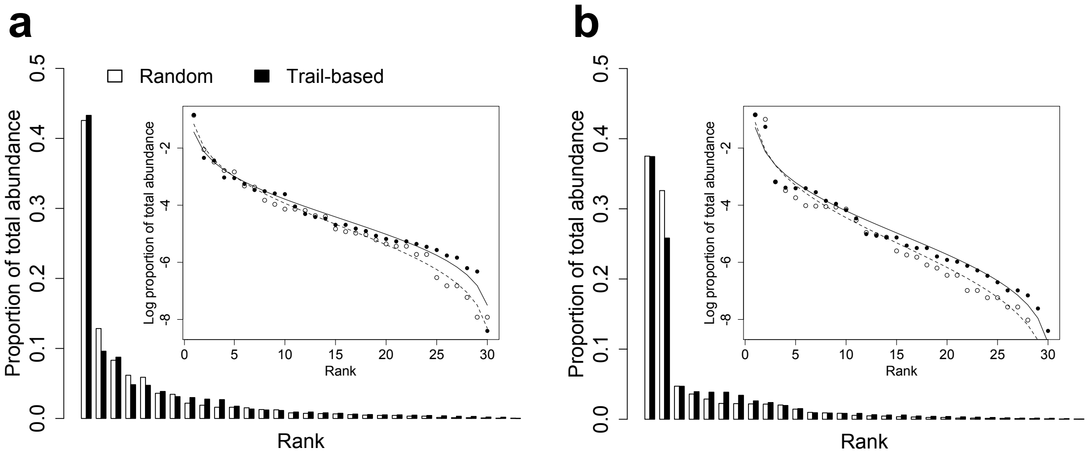

Figure 2.3. Rank abundance distributions and lognormal model fits (inset plots) for the (a) dry and (b) wet seasons. A set of 30 species was considered in order to facilitate comparison, with ranks based on RAIs measured at the survey level. Species are ranked from 1 to 30 on the x-axis according to decreasing proportion of total abundance.

During the dry season, trophic category was found to be the only predictor retained in the model with the lowest AIC value. Carnivore species, in particular, showed a significantly higher probability of being caught at trail placements (z = 1.96, P = 0.035), with a back-transformed estimate of 0.89 (95% CIs: 0.50 - 0.98). It is worth noting that the slender mongoose (*H. sanguinea*) was the only carnivore species for which RAIs at trail and random placements were not significantly different. In contrast, herbivores were more likely to show equal RAIs across paired trail and random placements (z = -2.54, P = 0.011). The probability for a species within this trophic category to have a higher RAI at trail placements was 0.25 (95% CIs: 0.08 - 0.55). The hippopotamus (*Hippopotamus amphibious*), giraffe (*Giraffa camelopardalis*) and dikdik (*Madoqua kirkii*) were the only herbivore species to show significantly higher RAIs at trail placements. The probabilities of insectivore and omnivore species having higher RAIs at trail placements were intermediate between those of carnivores and herbivores. The back-transformed probability for an insectivore species of having a higher RAI at trail placements was 0.5 (95% CIs: 0.12 - 0.88), whilst that for an omnivore species was 0.6 (95% CIs: 0.20 - 0.90). Finally, during the wet season, log body mass was the only predictor retained to describe significantly higher RAIs at trail placements, with larger species showing a higher probability than smaller ones (Figure 2.4).

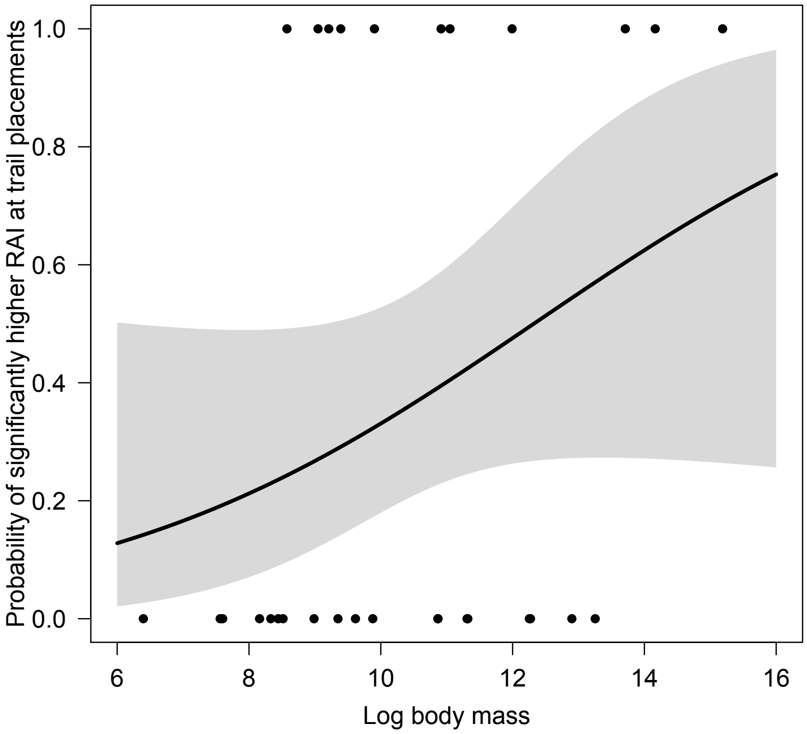

Figure 2.4. Influence of log body mass on the probability for a species to be caught significantly more often at trail placements during the wet season. The shaded polygon represents the 95% confidence interval surrounding the regression line and black dots represent the species-specific binomial responses used in the generalised linear model.

DISCUSSION

Non-random camera trap placement in the context of multi-species surveys violates a key principle of sampling theory: the random selection of sampling units (Wearn et al. 2013). Although the influence of placement strategy has been investigated in the past, few studies have implemented designs that specifically controlled for spatial or temporal confounding factors (Melo et al. 2012, Blake and Mosquera 2014, Di Bitteti et al. 2014), and none that we are aware of in savannah habitats. In our study, the random and trail-based surveys sampled the same locations at the same time, enabling us to test more rigorously the influence of placement strategy on the observed richness, composition and structure of a terrestrial mammal community. Although we did not have an exact reference community against which to compare our results, we were able to assess relative differences between community patterns resulting from random and trail-based camera trap placement strategies (Table 2.3).

Although choice of placement strategy did not seem to affect overall community structure, it did have a marginal effect on observed community richness and composition during the wet season and for lower levels of sampling effort. In particular, species known to occur at naturally low densities, such as the caracal and the African wild dog, tended to be detected only by the trail-based survey during the wet season, indicating that this placement strategy may be more preferable for species inventorying at times when vegetation density may be higher off trails. Despite this, neither of the placement strategies implemented in this study was able to record all 41 species detected overall, indicating that neither offered a completely optimal design for species inventorying. For instance, the klipspringer and the African wild dog were only detected by the trail-based survey while the ground pangolin only by the random one. Nevertheless, for studies that can implement extensive surveys (i.e. > 1400 camera trap days on average), random camera placements may eventually yield a more complete list of species, especially since game trails will also be sampled in proportion to their occurrence (Rowcliffe et al. 2013). Conversely, if sampling periods are short or the number of cameras available limited, trail-based camera placements may facilitate detection of more species, more rapidly.

The use of RAIs to determine species rankings within observed communities cannot be recommended owing to the uncertainty as to whether these are truly correlated with species density (Carbone et al. 2001, Jennelle et al. 2002). However, we were interested in assessing relative changes in species rankings between two surveys sampling the same locations at the same time. Our finding that species can show significant shifts in rank between two surveys adopting different placement strategies – reflecting relative changes in RAIs – supports previous conclusions (Srbek-Araujo and Chirello 2005, Harmsen et al. 2010, Wearn et al. 2013). For instance, Sollmann et al. (2013) showed that species-specific response to different types of "trap setups" biased RAIs drawn from camera trap data. We found that RAIs could be significantly higher at trail placements depending on trophic category or body size of the species in question during the dry and wet season, respectively, thereby influencing observed rank in the corresponding community.

Table 2.3. Advantages (pros) and disadvantages (cons) of random and game trail-based camera trap placement strategies in relation to different types of survey aims, based on a comparison carried out in Ruaha National Park, Tanzania.

	Community richness and composition		Species presence/Occupancy		Space/Habitat use	
Placement strategy	Pros	Cons	Pros	Cons	Pros	Cons
Random	• Detection of species that never use trails	• Slower to detect many species so greater effort needed to capture full community • Fewer species detected when dense vegetation	• More likely to detect species that never use trails	• Less likely to detect larger and carnivore species	• More landscape features sampled • More accurate characterisation of species preferences across wider landscape	• May need more sampling effort to obtain adequate sample size
Game trail-based	• Detect most species more rapidly	• Non-detection of species that never use trails	• More likely to detect larger bodied and carnivore species • More likely to detect species when vegetation is dense	• Less likely to detect species that never use trails	• Larger sample size for many species (particularly larger bodied, carnivores)	• Inferences will be restricted to trails

Carnivores, in particular, had significantly higher RAIs at trail placements during the dry season. Carnivore preference for trails is well known and has influenced the placement of camera traps since systematic surveys aimed at estimating abundance of rare and elusive felids were first implemented (Karanth et al. 1995). Despite this, the reasons underlying the preferential use of trails by carnivores remain less well understood, but causes may be grounded in optimal foraging theory, which dictates that individuals should attempt to maximise net energy gain per unit time, or minimise travel costs (Emlen 1966, MacArthur and Pianka 1966). For species that defend a territory or whose resources are heterogeneously distributed in space, such as most carnivores and some insectivores (e.g. the aardwolf), trails may represent cost-effective patrolling routes or links between areas of high resource abundance. In the case of RNP's large carnivores, the latter may correspond to areas close to the river where herbivores gather in the dry season.

In contrast, relative abundance indices for most herbivores did not differ between placement strategies. An important implication of this finding is that studies using trail placements so as to increase capture probabilities of carnivore species – in the context of mark-recapture analyses, for instance – may at the same time collect unbiased data on their potential prey. However, this may not be the case for all herbivore species, as shown by the significantly higher RAIs obtained for the giraffe, dikdik and hippopotamus at trail placements. Interestingly, while the former species may use trails as a consequence of its unique morphology, the second is known to be a territorial species whose use of trails may be linked to patrolling activities. Finally, hippopotamuses, which are primarily detected in proximity to the Great Ruaha River in the dry season, are known to follow trails between the water's edge and nocturnal grazing grounds.

A number of reasons may explain the positive relationship between species body mass and significantly higher RAIs measured at trail placements during the wet season. Firstly, it may be more energetically costly for larger bodied species to travel through the denser vegetation typically found at this time of the year outside of trails. Secondly, larger bodied species often create and maintain the network of trails occurring in the landscape, and may therefore use them out of habit. Finally, the size of trails used by a species may be proportional to its body size. Smaller species may favour narrower trails than the ones considered in this study (≥ 1 m in width), which may be used preferentially by larger bodied animals.

CONCLUSIONS

Our study has shown that, given adequate sampling effort (> 1400 camera trap nights), placement strategy is unlikely to affect inferences made at the community level. While differences in community richness were notable in the wet season and for lower levels of sampling effort, patterns of community composition and structure as revealed by random and game trail-based camera placements were similar overall. In contrast, and in agreement with previous work, placement strategy was found to influence capture rates of individual species, and especially those of carnivores and larger bodied species during the dry and wet season, respectively. Although our study was based in a relatively open east African landscape, our work should ideally be replicated in forested habitats, where, given the more cluttered nature of the habitat, it can be expected that differences in observed communities will be greater.

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SUPPORTING INFORMATION

Table S2.1. Species-specific variables used in generalised linear models investigating the determinants of high relative abundance indices at trail placements.

Table S2.2. Species-specific location shift between random and trail-based camera placements during the dry season.

Table S2.3. Species-specific location shift between random and trail-based camera placements during the wet season.

Table S2.1. Species-specific variables used in generalised linear models (GLMs) investigating the determinants of high relative abundance indices (RAIs) at trail placements. For each of 30 species, trophic category is given alongside social behaviour (solitary or social) and average body mass (in kg). Species for which the RAI at trail placements was found to be significantly higher than that at random placements were given a score of 1 whilst others were given a score of 0. The latter were used as response variables in season-specific GLMs with binomial errors and logit link functions.

Species	Trophic category[a]	Social behaviour	Mass[b]	Binomial response	
				Dry season	Wet season
Aardvark	Insectivore	Solitary	52.4	0	0
Aardwolf	Insectivore	Solitary	10.0	1	1
African civet	Omnivore	Solitary	12.0	1	1
Baboon	Omnivore	Social	15.0	0	1
Banded mongoose	Insectivore	Social	1.9	1	0
Bat-eared fox	Insectivore	Social	4.2	0	0
Black backed jackal	Carnivore	Social	8.5	1	1
Bush duiker	Herbivore	Solitary	19.5	0	0
Common genet	Omnivore	Solitary	2.0	1	0
Dikdik	Herbivore	Social	5.3	1	1
Eland	Herbivore	Social	570.0	0	0
Elephant	Herbivore	Social	3940.0	0	1
Giraffe	Herbivore	Social	900.0	1	1
Greater kudu	Herbivore	Social	214.0	0	0
Hippopotamus	Herbivore	Social	1418.0	1	1
Honey badger	Carnivore	Solitary	8.0	1	0
Impala	Herbivore	Social	52.5	0	0
Leopard	Carnivore	Solitary	55.0	1	1
Lesser kudu	Herbivore	Social	81.6	0	0
Lion	Carnivore	Social	161.5	1	1
Porcupine	Omnivore	Social	20.0	1	1
Serval	Carnivore	Solitary	11.5	1	0
Slender mongoose	Carnivore	Solitary	0.6	0	0
Spotted hyena	Carnivore	Social	63.0	1	1
Vervet monkey	Omnivore	Social	5.0	0	0
Warthog	Herbivore	Social	82.5	0	0
Waterbuck	Herbivore	Social	210.0	0	0
White-tailed mongoose	Carnivore	Solitary	3.5	1	0
Wild cat	Carnivore	Solitary	4.7	1	0
Zebra	Herbivore	Social	400.0	0	0

[a] Based on Kissling et al. (2014).

[b] Based on Smith et al. (2003).

Table S2.2. Species-specific location shift between random and trail-based camera placements during the dry season. Comparisons were based on pairwise Wilcoxon signed rank tests. These tested the null hypothesis that the distribution of pairwise differences (trapping rates at random placements minus those at trail placements) was symmetric about zero. The mean of the resulting normal distribution – termed the location shift – and the associated 95% confidence intervals were used to assess the level of significance ($\alpha = 0.05$) relative to zero.

		95% CI		
Species	Location shift	Lower	Upper	P-value
Aardvark	-0.79	-2.53	0.94	0.906
Aardwolf	-2.55	-3.43	-1.67	< 0.01
African civet	-1.70	-3.29	-0.10	< 0.05
Baboon	-1.79	-4.22	0.63	0.158
Banded mongoose	-2.49	-3.28	-1.69	< 0.01
Bat-eared fox	0.86	-3.27	5.00	0.755
Black backed jackal	-2.43	-4.07	-0.79	< 0.01
Bush duiker	1.69	-1.84	5.23	0.320
Common genet	-3.15	-6.29	0.00	< 0.05
Dikdik	-4.73	-7.74	-1.72	< 0.05
Eland	1.09	-2.91	5.08	0.789
Elephant	-1.43	-5.11	2.25	0.386
Giraffe	-4.08	-6.82	-1.35	< 0.05
Greater kudu	-2.22	-4.54	0.10	0.108
Hippo	-6.95	-11.95	-1.95	< 0.05
Honey badger	-1.68	-3.23	-0.13	< 0.05
Impala	-5.77	-17.64	6.11	0.386
Leopard	-2.54	-4.18	-0.90	< 0.01
Lesser kudu	-0.69	-4.76	3.38	0.834
Lion	-2.44	-4.44	-0.44	< 0.05
Porcupine	-2.54	-3.41	-1.67	< 0.05
Serval	-2.85	-4.03	-1.67	< 0.01
Slender mongoose	-0.72	-2.27	0.83	0.453
Spotted hyena	-3.70	-5.71	-1.68	< 0.001
Vervet monkey	-1.68	-5.41	2.04	0.683
Warthog	-0.45	-1.96	1.06	0.314
Waterbuck	0.90	-2.37	4.18	0.675
White tailed mongoose	-1.72	-3.34	-0.11	< 0.05
Wildcat	-5.30	-10.04	-0.56	< 0.05
Zebra	-0.92	-2.87	1.04	0.361

Table S2.3. Species-specific location shift between random and trail-based camera placements during the wet season. Comparisons were based on pairwise Wilcoxon signed rank tests. These tested the null hypothesis that the distribution of pairwise differences (trapping rates at random placements minus those at trail placements) was symmetric about zero. The mean of the resulting normal distribution – termed the location shift – and the associated 95% confidence intervals were used to assess the level of significance ($\alpha = 0.05$) relative to zero.

		95% CI		
Species	Location shift	Lower	Upper	P-value
Aardvark	-1.64	-4.92	1.64	0.326
Aardwolf	-2.46	-4.10	-0.82	< 0.05
African civet	-1.64	-2.44	-0.84	< 0.05
Baboon	-1.26	-2.53	-0.01	< 0.05
Banded mongoose	-1.14	-3.28	1.00	0.272
Bat-eared fox	0.14	-4.10	4.38	0.905
Black backed jackal	-2.50	-4.97	-0.03	< 0.05
Bush duiker	-1.64	-4.10	0.82	0.230
Common genet	-0.82	-2.46	0.82	0.246
Dikdik	-5.45	-9.26	-1.64	< 0.01
Eland	0.00	-2.07	2.07	0.500
Elephant	-14.87	-28.75	-1.00	< 0.05
Giraffe	-2.46	-4.10	-0.82	< 0.01
Greater kudu	-0.52	-2.46	1.43	0.623
Hippo	-7.50	-12.54	-2.46	< 0.001
Honey badger	0.50	-3.92	4.92	0.786
Impala	-2.46	-11.48	6.56	0.538
Leopard	-1.72	-2.52	-0.92	< 0.05
Lesser kudu	1.64	-1.64	4.92	0.684
Lion	-2.46	-3.60	-1.32	< 0.01
Porcupine	-1.65	-2.46	-0.85	< 0.01
Serval	0.66	-1.13	2.46	0.659
Slender mongoose	-1.64	-3.28	0.00	0.345
Spotted hyena	-4.10	-5.74	-2.46	< 0.001
Vervet monkey	-2.94	-10.80	4.92	0.416
Warthog	-1.51	-3.60	0.57	0.252
Waterbuck	-1.64	-3.28	0.00	0.345
White tailed mongoose	-1.64	-3.32	0.04	0.112
Wildcat	1.62	0.11	3.12	0.181
Zebra	0.64	-2.97	4.24	0.706

REFERENCES

Abade, L., D. W. Macdonald, and A. J. Dickman (2014). Using landscape and bioclimatic features to predict the distribution of lions, leopards and spotted hyaenas in Tanzania's Ruaha landscape. *PLoS One* **9**, e96261.

Ahumada, J. A., C. E. Silva, K. Gajapersad, C. Hallam, J. Hurtado, E. Martin, A. McWilliam, B. Mugerwa, T. O'Brien, F. Rovero, D. Sheil, W. R. Spironello, N. Winarni, and J. A. Andelman (2011). Community structure and diversity of tropical forest mammals: data from a global camera trap network. *Philosophical Transactions of the Royal Society B: Biological Sciences* **366**, 2703–2711.

Ahumada, J. A., J. Hurtado, and D. Lizcano (2013). Monitoring the status and trends of tropical forest terrestrial vertebrate communities from camera trap data: a tool for conservation. *PLoS One* **8**, e73707.

Akaike, H. (1974). A new look at the statistical model identification. *Automatic Control, IEEE Transactions* **19**, 716–723.

Blake, J. G., and D. Mosquera (2014). Camera trapping on and off trails in lowland forest of eastern Ecuador: does location matter? *Mastozoología Neotropical* **21**, 17–26.

Burnham, K. P., and D. R. Anderson (2002). *Model selection and multimodel inference: a practical information-theoretic approach*. Springer, New York.

Can, O. E., and I. Togan (2009). Camera trapping of large mammals in Yenice Forest, Turkey: local information vs. camera traps. *Oryx* **43**, 427–430.

Carbone, C., S. Christie, K. Conforti, T. Coulson, N. Franklin, J. R. Ginsberg,

M. Griffiths, J. Holden, K. Kawanishi, M. Kinnaird, R. Laidlaw, A. Lynam, D. W. Macdonald, D. Martyr, C. McDougal, L. Nath, T. O'Brien, J. Seidensticker, D. J. L. Smith, M. Sunquist, R. Tilson, and W. N. Wan Shahruddin (2001). The use of photographic rates to estimate densities of tigers and other cryptic mammals. *Animal Conservation* **4**, 75–79.

Chao, A., N. G. Gotelli, T. C. Hsieh, E. L. Sander, K. H. Ma, R. K. Colwell, and M. E. Ellison (2014). Rarefaction and extrapolation with Hill numbers: a framework for sampling and estimation in species biodiversity studies. *Ecological Monographs* **84**, 45–67.

Collins, S. L., K. N. Suding, E. E. Cleland, M. Batty, S. C. Pennings, K. L. Gross, J. B. Grace, L. Gough, J. E. Fargione, and C. M. Clark (2008). Rank clocks and plant community dynamics. *Ecology* **89**, 3534–3541.

Colwell, R. K., C. X. Mao, and J. Chang (2004). Interpolating, extrapolating, and comparing incidence-based species accumulation curves. *Ecology* **85**, 2717–2727.

Di Bitetti, M. S., A. Paviolo, and C. De Angelo (2014). Camera trap photographic rates on roads vs. off roads: location does matter. *Mastozoología Neotropical* **21**, 37–46.

Emlen, J. M. (1966). The role of time and energy in food preference. *The American Naturalist* **100**, 611–617.

Gopalaswamy, A. M., J. A. Royle, J. E. Hines, P. Singh, D. Jathanna, N. S. Kumar, and K. U. Karanth (2012). Program SPACECAP: software for estimating animal density using spatially explicit capture–recapture models. *Methods in Ecology and Evolution* **3**, 1067–1072.

Harmsen, B. J., R. J. Foster, S. Silver, L. Ostro, and C. P. Doncaster (2010). Differential use of trails by forest mammals and the implications for camera traps studies: a case study from Belize. *Biotropica* **42**, 126–133.

Hsieh, T. C., K. H. Ma, and A. Chao (2013). iNEXT online: interpolation and extrapolation. Version 1.0. <http://chao.stat.nthu.edu.tw/blog/software-download/>.

Jaccard, P. (1912). The distribution of the flora in the alpine zone. *New Phytologist* **11**, 37–50.

Jennelle, C. S., M. C. Runge, and D. I. MacKenzie (2002). The use of photographic rates to estimate densities of tigers and other cryptic mammals: a comment on misleading conclusions. *Animal Conservation* **5**, 119–120.

Jones, J. P. (2011). Monitoring species abundance and distribution at the landscape scale. *Journal of Applied Ecology* **48**, 9–13.

Karanth, K. U. (1995). Estimating tiger *Panthera tigris* populations from camera-trap data using capture-recapture models. *Biological Conservation* **71**, 333–338.

Kays, R., B. Kranstauber, P. Jansen, C. Carbone, M. Rowcliffe, T. Fountain, and S. Tilak (2009). Camera traps as sensor networks for monitoring animal communities. In: *IEEE 34th Conference on Local Computer Networks*, pp. 811-818. IEEE, Zurich.

Kays, R., S. Tilak, B. Kranstauber, P. A. Jansen, C. Carbone, J. M. Rowcliffe, T. Fountain, J. Eggert, and Z. He (2011). Monitoring wild animal communities with arrays of motion sensitive camera traps. *International Journal of Research and Reviews in Wireless Sensor Networks* **1**, 19–29.

Kingdon, J. (2013). *The Kingdon field guide to African mammals*. A&C Black, London.

Kissling, W. D., L. Dalby, C. Fløjgaard, J. Lenoir, B. Sandel, C. Sandom, K. Trøjelsgaard, and J. Svenning (2014). Establishing macroecological trait datasets: digitalization, extrapolation, and validation of diet preferences in terrestrial mammals worldwide. *Ecology and Evolution* **4**, 2913–2930.

MacArthur, R. H., and E. R. Pianka (1966). On optimal use of a patchy environment. *The American Naturalist* **100**, 603–609.

MacKenzie, D. I., J. D. Nichols, G. B. Lachman, S. Droege, A. J. Royle, and C. A. Langtimm (2002). Estimating site occupancy rates when detection probabilities are less than one. *Ecology* **83**, 2248–2255.

Meek, P. D., G. Ballard, and P. Fleming (2012). *An introduction to camera trapping for wildlife surveys in Australia*. Invasive Animals CRC, Canberra.

Meek, P. D., G. Ballard, A. Claridge, R. Kays, K. Moseby, T. O'Brien, A. O'Connell, J. Sanderson, D. E. Swann, M. Tobler, and S. Townsend (2014). Recommended guiding principles for reporting on camera trapping research. *Biodiversity and Conservation* **23**, 2321–2343.

Melo, G. L., J. Sponchiado, and N. C. Cáceres (2012). Use of camera-traps in natural trails and shelters for the mammalian survey in the Atlantic Forest. *Iheringia, Série Zoologia* **102**, 88–94.

Mugerwa, B., D. Sheil, P. Ssekiranda, M. van Heist, and P. Ezuma (2012). A camera trap assessment of terrestrial vertebrates in Bwindi Impenetrable National Park, Uganda. *African Journal of Ecology* **51**, 21–31.

O'Brien, T. G., M. F. Kinnaird, and H. T. Wibisono (2003). Crouching tigers, hidden prey: Sumatran tiger and prey populations in a tropical forest landscape. *Animal Conservation* **6**, 131–139.

O'Connell, A. F., J. D. Nichols, and K. U. Karanth (2010). *Camera traps in animal ecology: methods and analyses*. Springer, Tokyo.

Oksanen, J., F. G. Blanchet, R. Kindt, P. Legendre, P. R. Minchin, R. B. O’Hara, G. L. Simpson, P. Solymos, M. H. M. Stevens, and H. Wagner (2013). Package ‘vegan’: community ecology package. Version 2.0. <http://cran.r-project.org/web/packages/vegan/index.html>.

QGIS Development Team (2013). QGIS Geographic Information System Open Source Geospatial Foundation Project <http://qgis.osgeo.org>.

R Development Core Team (2014). R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria <http://www.R-project.org/>.

Rovero, F., and A. R. Marshall (2009). Camera trapping photographic rate as an index of density in forest ungulates. *Journal of Applied Ecology* **46**, 1011–1017.

Rovero, F., F. Zimmermann, D. Berzi, and P. Meek (2013). "Which camera trap type and how many do I need?" A review of camera features and study designs for a range of wildlife research applications. *Hystrix, the Italian Journal of Mammalogy* **24**, 148–156.

Rovero, F., E. Martin, M. Rosa, J. A. Ahumada, and D. Spitale (2014). Estimating species richness and modelling habitat preferences of tropical forest mammals from camera trap data. *PLoS One* **9**, e103300.

Rowcliffe, J. M., R. Kays, C. Carbone, and P. A. Jansen (2013). Clarifying assumptions behind the estimation of animal density from camera trap rates. *The Journal of Wildlife Management* **77**, 876–876.

Smith, F. A., S. K. Lyons, S. M. Ernest, K. E. Jones, D. M. Kaufman, T. Dayan, P. A. Marquet, J. H. Brown, and J. P. Haskell (2003). Body mass of late quaternary mammals: Ecological Archives E084-094. *Ecology* **84**, 3403.

Sollmann, R., M. M. Furtado, B. Gardner, H. Hofer, A. T. Jácomo, N. M. Tôrres, and L. Silveira (2011). Improving density estimates for elusive carnivores: accounting for sex-specific detection and movements using spatial capture–recapture models for jaguars in central Brazil. *Biological Conservation* **144**, 1017–1024.

Sollmann, R., M. M. Furtado, H. Hofer, A. T. Jácomo, N. M. Tôrres, and L. Silveira (2012). Using occupancy models to investigate space partitioning between two sympatric large predators, the jaguar and puma in central Brazil. *Mammalian Biology-Zeitschrift für*

Säugetierkunde **77**, 41–46.

Sollmann, R., A. Mohamed, H. Samejima, and A. Wilting (2013). Risky business or simple solution – Relative abundance indices from camera-trapping. *Biological Conservation* **159**, 405–412.

Srbek-Araujo, A. C., and A. G. Chiarello (2005). Is camera-trapping an efficient method for surveying mammals in Neotropical forests? A case study in south-eastern Brazil. *Journal of Tropical Ecology* **21**, 121–125.

Stolberger, S. (2012). *Ruaha National Park: an intimate view*. Sue Stolberger, Tanzania.

Tobler, M. W., S. E. Carillo-Percastegui, R. Leite Pitman, R. Mares, and G. Powell (2008). An evaluation of camera traps for inventorying large- and medium-sized terrestrial rainforest mammals. *Animal Conservation* **11**, 169–178.

Walsh, M. (2000). The development of community wildlife management in tanzania: Lessons from the Ruaha ecosystem. In *African Wildlife Management in the New Millenium*. Mweka, Tanzania.

Wearn, O. R., J. M. Rowcliffe, C. Carbone, H. Bernard, and R. M. Ewers (2013). Assessing the status of wild felids in a highly-disturbed commercial forest reserve in Borneo and the implications for camera trap survey design. *PLoS One* **8**, e77598.

Wilson, J. B. (1991). Methods for fitting dominance/diversity curves. *Journal of Vegetation Science* **2**, 35–46.

Chapter 3

Applying a random encounter model to estimate lion density from camera traps in Serengeti National Park, Tanzania

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- Running head -

Density estimation of Serengeti lions

- Title -

Applying a random encounter model to estimate lion density from camera traps in Serengeti National Park, Tanzania

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ABSTRACT

The random encounter model (REM) is a novel method for estimating animal density from camera trap data without the need for individual recognition. It has never been used to estimate the density of large carnivore species, despite these being the focus of most camera trap studies worldwide. In this context, we applied the REM to estimate the density of female lions (*Panthera leo*) from camera traps implemented in Serengeti National Park, Tanzania, comparing estimates to reference values derived from pride census data. More specifically, we attempted to account for bias resulting from non-random camera placement at lion resting sites under isolated trees by comparing estimates derived from night versus day photographs, between dry and wet seasons, and between habitats that differ in their amount of tree cover. Overall, we recorded 169 and 163 independent photographic events of female lions from 7,608 and 12,137 camera trap days carried out in the dry season of 2010 and the wet season of 2011, respectively. Although all REM models considered over-estimated female lion density, models that considered only night-time events resulted in estimates that were much less biased relative to those based on all photographic events. We conclude that restricting REM estimation to periods and habitats in which animal movement is more likely to be random with respect to cameras can help reduce bias in estimates of density for female Serengeti lions. We highlight that accurate REM estimates will nonetheless be dependent on reliable measures of average speed of animal movement and camera detection zone dimensions.

INTRODUCTION

Camera traps are used worldwide to answer a range of questions relevant to ecology and conservation (O'Connell et al. 2010, Meek et al. 2014). A common aim of many camera trap surveys is estimating the density of a target species within an area of interest. To this end, recent spatially explicit capture-recapture (SECR) methods, which combine both the spatial and temporal information contained in photographs of recognizable individuals, have provided unbiased estimates of density for marked species, i.e., those for which animals are individually recognizable (Borchers and Efford 2008, Royle et al. 2009, Gardner et al. 2010, Gopalaswamy et al. 2012). Spatially explicit capture-recapture analysis is now supported by a substantial body of literature mainly focusing on spotted and striped felids (Sollmann et al. 2011, Gray and Prum 2012, Athreya et al. 2013). In contrast, no well-established methods exist for estimating the density of unmarked species using camera traps (Carbone et al. 2001, Jennelle et al. 2002, Chandler and Royle 2013), despite these representing the majority of species likely to be photographed (Tobler et al. 2008).

Rowcliffe et al. (2008) proposed a random encounter model (REM) that describes the rate of contact between moving animals and static camera traps to estimate species density. The REM requires a species encounter rate (sensu Carbone et al. 2001) to be estimated, along with a camera detection zone specified by its radius and angle, and an estimated average speed of movement for the target species. A key assumption of the model is that cameras are placed randomly with respect to animal movement (Rowcliffe et al. 2013), meaning that they should not be targeted so as to inflate, or deflate, encounter rates. Studies using the REM have been implemented by deploying cameras in systematic or fully randomized arrays (Rovero and Marshall 2009, Manzo et al. 2012), with camera placement determined a priori by precise geographical coordinates rather than influenced by the presence of features that may increase capture probability (Rowcliffe et al. 2008, Rovero et al. 2013).

To date, however, the REM has never been used to estimate the density of a large carnivore species (Foster and Harmsen 2012). We applied the model to estimate the density of female lions (*Panthera leo*) from an extensive camera trap survey implemented in Serengeti National Park, Tanzania, comparing estimates to reference values derived from pride census data (Schaller 1972, Bygott et al. 1979, Packer et al. 2005). As a threatened and unmarked large carnivore for which reliable estimates of abundance or density are difficult to obtain (Ogutu et al. 2006, Funston et al. 2010, Durant et al. 2011, Groom et al. 2014), the lion represents a suitable candidate species on which to test the REM. Indeed, given the decline of the species across Africa over the past decades (Riggio et al. 2013), it has become important to test the reliability of potential density estimation methods.

Importantly, the Serengeti camera trap survey was not designed with the REM in mind. Despite the use of a gridded design, the low tree density encountered in grassland habitat resulted in cameras often being placed on isolated trees whose shade attracted lions during the day, thus representing a potential violation of the random placement assumption. We assessed the effect of this known source of bias by comparing the accuracy of REM estimates derived from night-only versus all photographs, between wet and dry seasons, and across habitat types that differed in their amount of tree cover. During the night, during the wet season, and in more densely wooded habitat, lions are less likely to seek shade under trees, and we expected camera placements on trees to be closer to random with respect to lion movement. We anticipated that REM estimates derived from data filtered by these factors would show improved accuracy when compared to reference densities.

STUDY AREA

The study area encompasses 1,125 km^2 of the Serengeti National Park, Tanzania, and was located within the 25,000-km^2 Serengeti–Mara ecosystem (Figure 3.1). It is marked by a southeast-to-northwest gradient of rainfall and soil type (Norton-Griffiths 1975), which creates a transition from short-grass plains in the southeast (hereafter, grassland) to woodlands in the north (Packer et al. 2005). Lion density is largely limited by food availability in the dry season when prey biomass is at an annual low (Schaller 1972, Bertram 1975, Packer et al. 2005).

Lions live in gregarious groups known as prides, which are composed of related females, their dependent offspring, and 1 or more males (Scheel and Packer 1991, Packer et al. 2005). The latter form coalitions that can reside in, and distribute their time across, more than 1 pride (Schaller 1972, Bygott et al. 1979). In contrast, nomads do not maintain a territory and move great distances through the ecosystem (Schaller 1972). The population has been monitored continuously since 1974 (Bygott et al. 1979, Packer et al. 2001), and several prides have been monitored since 1966 (Schaller 1972). Since 1984, 1 female member of each study pride was radio-collared, with all subsequent monitoring relying on a combination of radio telemetry and opportunistic sightings (Mosser et al. 2009).

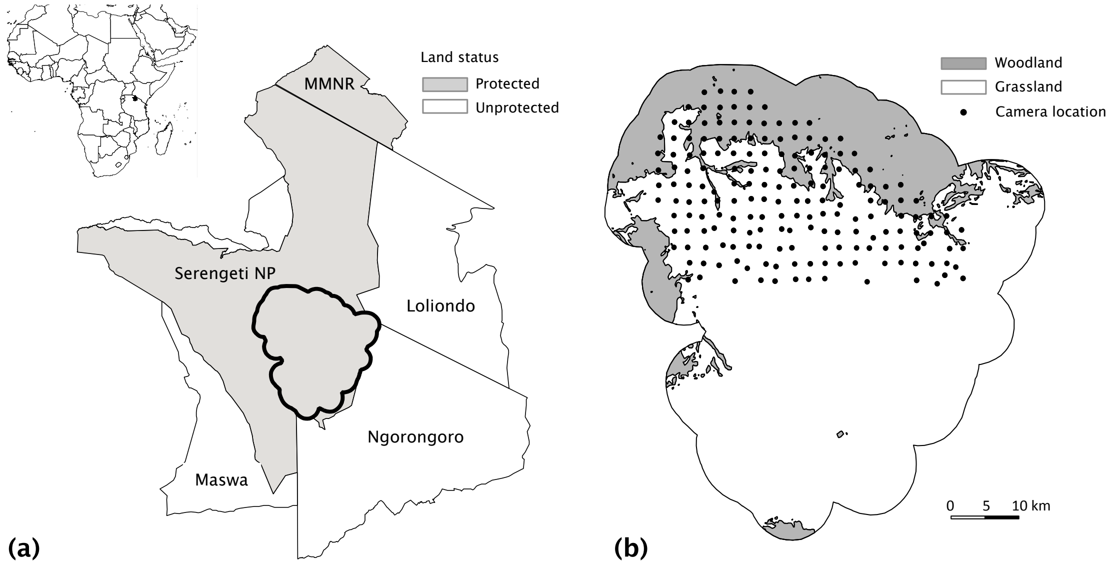

Figure 3.1. (a) Location of the Serengeti Lion Project study area (black outline) in northern Tanzania and (b) layout of the camera trap grid across woodland and grassland habitats. The Serengeti-Mara ecosystem encompasses key protected lion populations in Serengeti National Park (NP) and the Masai Mara National Reserve (MMNR) in Kenya.

METHODS

Camera Trap Survey

The data used in this study form part of an on-going camera trap survey implemented by the Serengeti Lion Project (SLP; Swanson et al. 2015). We consider 2 3-month blocks, 1 in the dry season of 2010 (Aug–Oct) and 1 in the wet season of 2011 (Mar–May), during which 168 and 167 camera locations were defined as active, respectively (Figure 3.1). We deployed camera traps (ScoutGuard SG595, Boly Media Communications, Santa Clara, CA, USA) at the centre of 5-km^2 grid cells, resulting in an average spacing of 2.3 km. This cell size aimed to ensure a minimum number of 5 traps per pride home range. In the case of the REM, spatial autocorrelation between neighbouring cameras is not considered a problem because the approach focuses on contact rates between cameras placed randomly with reference to animal movement. We used a handheld global positioning system (GPS) device to locate cell centroids and placed each camera trap on the closest tree within a 1-km radius of the corresponding point. If no trees were located within that distance, we attached cameras to man-made poles (8.7% of camera placements).

Camera settings were chosen as part of a large-scale, multi-species survey and were not specific to lions (Swanson et al. 2015). During the dry season, camera traps were programmed to take a sequence of 3 pictures per trigger during the day and at night. During the wet season, cameras took only 1 picture per trigger at night. We stress that this difference is unlikely to have resulted in bias because female lions were observed in the first of 3 photographs in 98.6% of events taken during the day. As a result, the number of pictures per trigger is unlikely to influence lion detection probability. In both seasons, there was an arbitrary 1-minute delay between consecutive triggers. The date and time of capture were automatically stamped onto each image. Although the camera model used an incandescent flash for night-time pictures, it is unlikely to have modified the behaviour of lions, which in the Serengeti are habituated to humans and research equipment.

We initially processed camera trap images to extract and quality control date and time metadata. We then imported the images into the Snapshot Serengeti (see www.snapshotserengeti.org) citizen science website for content classification. The latter combined multiple classifications of each image to yield high accuracy determinations of species (see Swanson et al. 2015, for more details).

Reference Densities

We calculated reference densities for female lions in grassland and woodland habitats for both the dry season of 2010 and the wet season of 2011. Habitat delineation was based on a classification of Landsat images (LPDAAC, USGS/EROS, Sioux Falls, SD, USA) into 24 vegetation assemblages by Reed et al. (2009) using the method put forward by Grunblatt et al. (1989). The Serengeti GIS and Data Centre later grouped these assemblages into 4 broad vegetation types based on percentage tree canopy cover (51–100% = dense woodland/forest; 21–50% = open woodland; 2–20% = savannah; less than 2% = grassland; available at www.serengetidata.org). In this study, we combined the dense woodland/forest and open woodland categories to define woodland polygons, and used the categories grassland and savannah to define grassland polygons.

At the time of study, 23 prides were known to use the study area and were being intensively monitored by the SLP. Each pride is generally located using radio telemetry and observed directly at least once every 2 weeks. Unlike camera trap images, direct observation of lions allows for individual recognition from natural facial markings (Packer and Pusey 1993), and thus enables near-perfect knowledge of pride size and composition. In particular, the size of the female component of each study pride (excluding cubs) is known with a very high level of confidence. Our study does not consider a small number of transient nomadic females, which are known to remain in the study area for very short periods of time only (Packer et al. 2005).

Although a number of Serengeti prides restrict their activities exclusively to grassland habitat (n = 8), pride home ranges generally straddle both habitat types (n = 15). Failure to account for this is likely to lead to bias in habitat-specific female densities. To determine each pride's contribution to female lion abundance in woodland and grassland habitats, we multiplied the known number of pride females by the proportion of the corresponding 75% home range that overlapped with either habitat type, which we denote as p. Since p is likely to vary seasonally for each pride owing to changing prey availability, we estimated seasonal 75% home ranges from pride-specific utilization distributions (UDs) drawn from the spatial coordinates of direct observations collected over the dry season of 2010 (Jun–Oct) and the wet season of 2011 (Nov–May), as per Mosser et al. (2009). Thus, for each pride, we obtained seasonal values of p, which we assumed reflected seasonal changes in the contribution to female lion abundance in woodland and grassland habitats. We estimated pride UDs using reference bandwidths (Silverman 1986) from functions implemented in the R package adehabitatHR

(Calenge 2006). We defined 75% home ranges as the minimum area over which the probability of relocating a pride was equal to 0.75 (Mosser et al. 2009, Calenge 2006).

For both grassland and woodland habitats, we calculated seasonal reference density of female lions D_{ref} as:

$$D_{ref} = \sum_{i=1}^{M}(N_i \times p_i)/A \qquad \text{eq 1}$$

in which M is the total number of lion prides with home ranges overlapping the habitat polygon, N_i is the total number of female lions within pride i (with $i \in$ M), p_i is the proportion of pride i's 75% home range overlapping the habitat polygon, and A is the habitat area effectively sampled by the camera trap grid. The latter was estimated by adding a buffer w equal to half the mean home range diameter of prides within the corresponding habitat to the camera trap grid hull (i.e., polygon obtained by joining the outer camera locations). We acknowledge that choice of buffer width for each habitat is the main source of uncertainty in our estimation of reference densities. To account for this, we derived reference density values for buffer widths corresponding to the 95% confidence limits of the corresponding habitat-specific mean home range radius. The resulting 95% confidence intervals surrounding our reference density values reflect the uncertainty associated with the estimation of A.

REM Parameterization

We used the following REM equation to obtain density estimates from camera trap encounter rates (Rowcliffe et al. 2008: equation 4):

$$D = \frac{y}{t} \cdot \frac{\pi}{Vr(2+\theta)} \qquad \text{eq 2}$$

in which y is the number of independent photographic events, t is total camera survey effort, V is average speed of animal movement, and r and θ are the radius and angle of the camera trap detection zone, respectively.

We considered only camera trap photographs taken in the dry season of 2010 (Aug–Oct) and the wet season of 2011 (Mar–May). We did not include images of male lions in our analyses owing to our reduced ability to accurately estimate reference male densities. We defined an independent contact with a camera as a female lion entering and exiting the field of view. Therefore, we considered consecutive photographic events of an individual lion remaining stationary in front of a camera as the same event. We calculated survey effort as the total number of camera hours, and obtained encounter rates by dividing the total number of independent photographic events of female lions by total survey effort. We defined night-time photographic events as those occurring between 1800 and 0600.

We carried out ex-situ field trials to determine the dimensions of the camera detection zone. To estimate camera radius r, we approached a test camera directly from the front and on all fours 10 times, and measured the distance from the camera to the location at first trigger for each approach. For camera angle θ, we carried out 10 paired approaches (1 from each side) perpendicular to the sensor beam at a distance of 5 m and recorded the location at first trigger. For each resulting location, we took a bearing using a compass placed on a flat surface directly below the camera. We recorded detection angle as the angle formed by the mean compass bearings taken on each side. We averaged values across trials to obtain values r and θ. We also carried out a sensitivity analysis to determine the effect of a 1% change in the value of r or θ on estimated density.

We estimated average distance moved per hour by female lions (hereafter, speed) from 4-day continuous follows of individual Serengeti prides carried out between September 1984 and December 1987 (see Packer et al. 1990, Scheel and Packer 1991). During these surveys, observers remained at least 200 m away from lions at all times. We derived distance moved from car odometer readings. For the purpose of this study, we assigned followed prides to woodland or grassland habitat based on the dominant habitat type within their 75% home range. For each season, we averaged hourly movement rate across prides of the same habitat to obtain average speed of movement during the 24-hour period (V_{all}) and at night (V_n).

Although lions are considered a social species and are often encountered as part of a pride, we chose not to define individual events as group contact events whereby REM density is multiplied by average group size (Rowcliffe et al. 2008, Zero et al. 2013). Our view is analogous to that put forward in the context of distance sampling of clustered animals. Thomas et al. (2010) acknowledge that treating grouped individuals as independent may sometimes be necessary if accurate group counts are not easily obtained, or if groups are not cohesive, as is the case for lions. In this case, variance surrounding the REM estimates will be inflated, but estimates remain unbiased (Thomas et al. 2010).

Density Estimation

We defined 4 season-habitat subsets for which to estimate female lion densities: dry season-grassland (D-G), dry season-woodland (D-W), wet season-grassland (W-G), and wet season-woodland (W-W). We extracted habitat-specific camera points from corresponding habitat polygons (Figure 3.1) and derived separate REM estimates from all and night-time only photographic events.

We computed overall variance of REM density estimates using the delta method (Seber 1982). The latter incorporated variance associated with the encounter rate (estimated by re-sampling camera locations with replacement 10,000 times, as per Rowcliffe et al. 2008), as well as standard errors associated with the independent estimation of parameters V, r, and θ. We used the resulting 95% confidence intervals to assess whether REM estimates differed significantly from reference values. We used percentage differences from reference densities to assess bias in REM estimates. We carried out all analyses in R version 3.0.3 (http://cran.r-project.org, accessed 2 Oct 2013).

RESULTS

Prides with home ranges straddling both grassland and woodland habitat accounted for 65.2% and 60.9% of all monitored prides during the dry and the wet season, respectively (Table S3.1). Estimated reference female lion abundance was 102.7 for dry season-grassland, 47.2 for dry season-woodland, 112.3 for wet season-grassland, and 29.7 for wet season-woodland. Estimated survey area for grassland habitat was 824.9 km^2 and 904.8 km^2 during the dry and wet season, respectively. For woodland habitat, estimated surveyed area was 332.6 km^2 and 358.6 km^2 during the dry and wet season, respectively. Mean home range area was greatest in grassland habitat during the wet season (Table 3.1).

Table 3.1. Mean 75% pride home-range kernel area (HR; in km^2) of lions in the Serengeti Lion Project study area during the dry season of 2010 and the wet season of 2011, and buffer width added to the habitat polygon for the different season-habitat combinations considered (*w;* in km). D-G = dry season-grassland; D-W = dry season-woodland; W-G = wet season-grassland; W-W = wet season-woodland.

Season-habitat	No. of prides	Mean HR area	*w*	*w* 95% CI
D-G	13	49.1	4.0	2.6–5.2
D-W	10	46.6	3.9	2.8–5.3
W-G	13	78.0	5.0	3.5–6.2
W-W	10	51.6	4.1	2.2–5.0

We obtained 169 independent events of female lions from 7,608 camera trap days in the dry season, including 55 taken at night (see Table 3.2 for a summary of events recorded per season-habitat combination). For the wet season, 163 independent events were recorded over 12,137 camera trap days, including 73 at night. We used follow data from 3 woodland and 4 grassland prides to estimate habitat-specific average speed of lion movement in the dry and wet season, respectively (Table 3.2; Table S3.2). Average speed during both the 24-hour period and at night was highest in grassland habitat during the wet and dry seasons (Table 3.2). Estimates for camera detection radius and angle were 14.42 m (SE = 0.778 m) and 50.12° (SE = 1.557°), respectively. Our sensitivity analysis revealed that, all else remaining equal, a 1% change in detection radius resulted in a 1% change in density, whereas the same perturbation of the detection angle value only resulted in a 0.3% change in estimated density.

Table 3.2. Camera effort (in days) and number of independent photographic events of female Serengeti lions recorded in total and at night only for the different habitats considered during the dry season of 2010 and the wet season of 2011. V_{all} and V_n represent average speed of lion movement (in km/hr) over the 24-hour period and at night (±SE), respectively, and were derived from 96-hour continuous follows of selected prides. D-G = dry season-grassland; D-W = dry season-woodland; W-G = wet season-grassland; W-W = wet season-woodland.

Season-habitat	Effort	Total no. of events	No. night-time events	V_{all}	V_n
D-G	5,348	131	33	0.173 (±0.012)	0.287 (±0.017)
D-W	2,260	38	22	0.135 (±0.017)	0.275 (±0.020)
W-G	8,424	140	56	0.189 (±0.009)	0.307 (±0.013)
W-W	3,713	23	17	0.126 (±0.021)	0.288 (±0.028)

All REM models considered over-estimated Serengeti female lion density but to varying degrees (Table 3.3; Figure 3.2). Models that considered only night-time events resulted in estimates that were much less biased relative to those based on all photographic events. Estimates from all events were also significantly different from reference density values for all season-habitat combinations except in woodland habitat during the wet season. In contrast, confidence intervals associated with night-time REM estimates and reference densities overlapped for all season-habitat combinations. Although restricting data to night-time records had the strongest effect on accuracy, the effect of season was also notable, with wet season estimates based on all events being less biased than dry season estimates (Figure 3.2). When considering all events, estimates from woodland habitat were closer to reference values in both seasons.

Table 3.3. Random encounter model (REM) and reference density (D_{ref}) estimates (with 95% CI) for female Serengeti lions in grassland and woodland habitats during the dry season of 2010 and the wet season of 2011. D-G = dry season-grassland; D-W = dry season-woodland; W-G = wet season-grassland; W-W = wet season-woodland.

Season-habitat	REM all events		REM night events		D_{ref}	
	Estimate	95% CI	Estimate	95% CI	Estimate	95% CI
D-G	0.467	0.391–0.542	0.142	0.094–0.190	0.124	0.111–0.141
D-W	0.375	0.211–0.539	0.213	0.096–0.330	0.142	0.111–0.170
W-G	0.294	0.222–0.366	0.145	0.109–0.181	0.124	0.112–0.142
W-W	0.147	0.093–0.201	0.095	0.050–0.139	0.083	0.072–0.120

DISCUSSION

Estimates of animal density form the basis of many monitoring programs and often determine allocation of conservation efforts (Jones et al. 2013). Although camera traps offer a cost-effective way of gathering information on multiple species, methods for estimating density remain largely focused on marked species. In this context, the REM offers a simple framework that is potentially suited to a wider range of species. However, Foster and Harmsen (2012) suggest that the model's assumption of random placement of cameras with respect to animal movement will often not be achievable for most species, and territorial large carnivores in particular. Countering this assessment, our study has shown that restricting REM estimation to periods and habitats in which animal movement is more likely to be random with respect to cameras can help reduce bias in estimates of density for female Serengeti lions. Nevertheless, we emphasize that despite this approach, our estimates remain biased to some degree in all season-habitat combinations, highlighting the need for truly random placement with respect to animal movement, as well as reliable estimates of average speed of animal movement and camera detection zone dimensions.

Lion movement in the Serengeti is primarily influenced by the distribution and density of prey (Hopcraft et al. 2005, Packer et al. 2005, Mosser and Packer 2009) but also at small scales by the distribution of landscape features, and trees in particular. The latter represent an important source of shade in a largely open savannah habitat. Thus, although the approximate locations of camera points across the study landscape were chosen using a systematic grid approach, preferential positioning of camera traps on trees at a finer scale represented a violation of the REM's random placement assumption. However, using prior knowledge of lion behaviour, we hypothesized that this violation would be less severe when tree cover is used less disproportionately by lions, specifically during the night, during the wet season, and in woodland habitat. By estimating densities using data filtered by these factors, we found that all 3 did indeed reduce bias, and most especially the exclusion of daytime records, which was alone sufficient to generate estimates that were not significantly different from reference in any habitat-season combination. In contrast, estimates obtained using both day and night-time data showed substantial and significant over-estimation in all cases. Given reliable estimates of average speed of animal movement and camera detection zone dimensions, these results highlight the capacity for the REM to provide unbiased density estimates for a large carnivore species, but only if the assumption of random distribution of cameras and animals relative to one another is met.

The REM performed well relative to other methods used to derive absolute lion densities in the past. Estimates were more precise (i.e., narrower confidence intervals) than those obtained for Serengeti lions using distance sampling (Durant et al. 2011), which also required a higher level of sampling effort. Similarly, the use of sight-resight methods to estimate lion density in Kenya's Masai Mara was described by Ogutu et al. (2006) as "costly and time-consuming" owing to the necessity for accurate recognition of individual animals. In contrast, the REM may offer a promising and more cost-effective alternative to estimating animal density, provided model parameters are estimated accurately.

In line with this, a current drawback of the REM is its reliance on independent estimates of animal speed of movement and camera detection zone dimensions. Even in the case of the well-studied Serengeti lion population, estimates for these parameters still bear an unknown level of error. For example, camera sensitivity may be different for a 70-kg human than for a 200-kg lion. Although a method does exist that enables extraction of species-specific camera detection zone dimensions directly from the raw images (Rowcliffe et al. 2011), the camera model and settings used in this study precluded its application. Detection radius has been shown to decrease in the wet season, which could have affected REM estimates given that density is directly proportional to this parameter, as shown by our sensitivity analysis. In contrast, estimated density was found to be less sensitive to changes in camera detection angle.

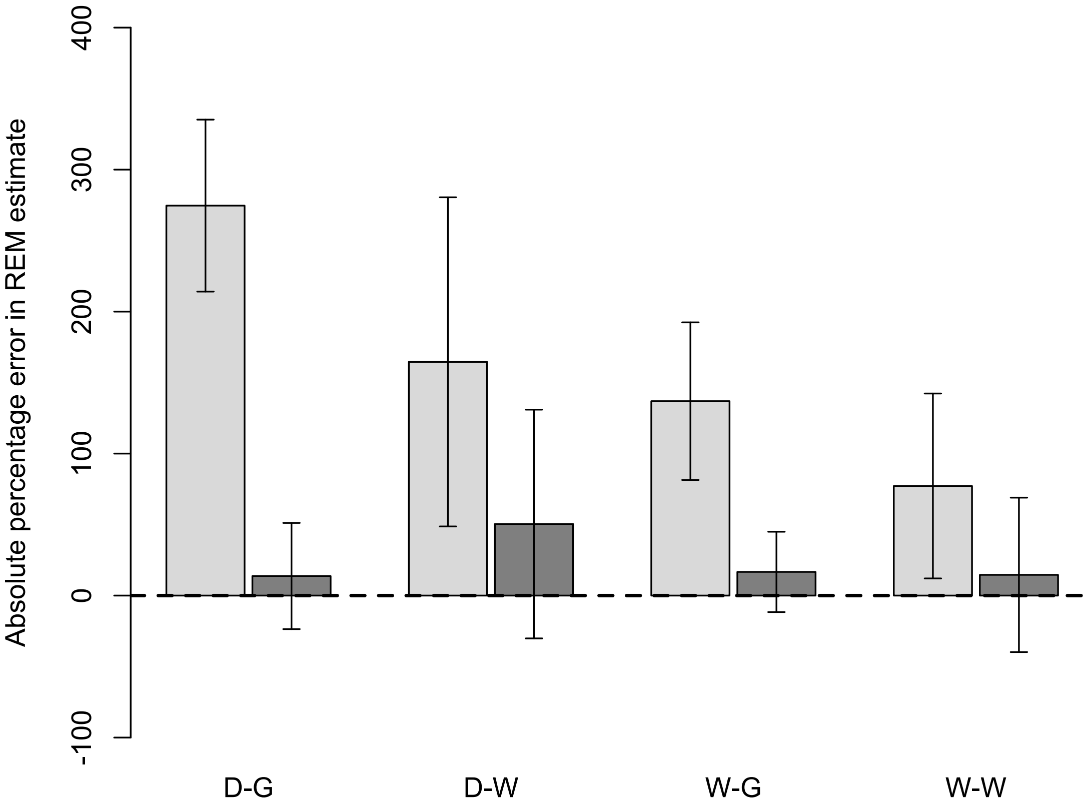

Figure 3.2. Absolute percentage errors associated with random encounter model (REM) estimates of female lion density in the Serengeti Lion Project study area during the dry season of 2010 and the wet season of 2011. Reference density is symbolized by the dashed horizontal line at 0% error. Bars represent errors in the estimates derived from all (light grey) or night-time only (dark grey) photographic events. Season-habitat combinations are defined as follows: dry season-grassland (D-G), dry season-woodland (D-W), wet season-grassland (W-G), and wet season-woodland (W-W). Error brackets represent the percentage errors of 95% confidence intervals associated with REM estimates.

For the same reason, obtaining accurate estimates of animal speed of movement is crucial to the model's success. Despite this, studies using camera traps often possess limited information on the target species, including speed of movement. For example, Manzo et al. (2012) used day range estimates from Poland to estimate the density of European pine marten (*Martes martes*) in central Italy using the REM. Although we derived our estimates of average speed of lion movement from data collected nearly 30 years ago, there is no evidence that lion ranging patterns have changed in the interim. The intensive observations in the 1980s and the current camera trap survey were both conducted in the same general area, where there has been no substantial change in prey species (Packer et al. 2005, Sinclair et al. 2007) and human impacts have remained consistently low. Thus, given the scarcity of GPS collar data for Serengeti lions, we believe our estimates of speed to be adequate for the present study.

Our ability to assess the REM as a density estimation tool for Serengeti lions is dependent on reliable reference density values. Although we cannot exclude the possibility that a small number of itinerant females remain unaccounted for, our knowledge of female lion numbers in the study area is very close to complete because of intensive and on-going monitoring by the SLP. We acknowledge that defining the area sampled by the camera trap grid remains the primary source of uncertainty in our estimation of reference densities. However, we believe the range of buffer widths over which we estimated reference densities adequately reflects this uncertainty.

MANAGEMENT IMPLICATIONS

Obtaining accurate estimates of animal density remains a constant challenge in the management and conservation of threatened large carnivores, and unmarked species in particular. We have shown that a relatively simple model, the REM, may be used to estimate the density of a territorial and unmarked large carnivore from camera trap data on the condition that clear violations of the model's key assumption are identified and reduced as much as possible using prior knowledge of animal behaviour. Indeed, the latter may be used to identify time periods (e.g., day or night) or camera locations (e.g., habitat type) that satisfy the requirement for randomness of cameras with respect to animals. Although we demonstrated this approach on existing camera trap data that were not collected with REM analysis in mind, we stress that, if available, knowledge of animal movement patterns should preferably guide REM survey design so as to avoid violations of the random placement assumption from the study onset. In the case of Serengeti lions, this suggests avoiding preferential positioning of camera traps on isolated trees. However, more generally for any species, we do not recommend application of the REM to data obtained from baited or lured cameras, from cameras placed preferentially on trails, watering points, mineral licks, outside of dens and known resting sites, or at any other landscape feature that may inflate or deflate capture rates. Nevertheless, our findings open up possibilities for the application of the REM to a broader range of unmarked species. In line with this, efforts are currently underway to streamline REM parameter estimation from the raw camera trap images (Rowcliffe et al. 2014), and it is hoped that these advances will greatly enhance standardization of the method as well as increase the accuracy of future estimates.

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SUPPORTING INFORMATION

Table S3.1. Pride-specific information used to calculate season-habitat reference densities.

Table S3.2. Number of follow hours and cumulative distance moved used to estimate average speed of lion movement.

Table S3.1. Pride-specific information used to calculate season-habitat reference densities (excluding cubs).

	75% HR contour area		Prop. HR in grassland		Dominant habitat in HR		Number of female lions	
Pride code	Dry	Wet	Dry	Wet	Dry	Wet	Dry	Wet
BF	106	118	0.34	0.74	W	G	8	7
BH	14	16	0.54	0.33	G	W	1	1
CS	24	40	0.49	0.56	W	G	4	5
CV	63	83	0.76	0.95	G	G	14	13
EP	56	95	1.00	1.00	G	G	2	2
JK	29	44	1.00	1.00	G	G	3	3
KB	29	66	0.29	0.49	W	W	6	7
LL	49	79	0.21	0.28	W	W	8	7
MH	82	73	0.76	0.93	G	G	3	1
MK	51	78	0.89	0.90	G	G	11	9
MM	42	130	0.76	0.88	G	G	3	3
MY	26	35	0.77	0.81	G	G	6	7
N3	50	44	1.00	1.00	G	G	2	2
PN	55	88	1.00	1.00	G	G	8	10
S#	24	45	1.00	1.00	G	G	18	17
SB	73	73	1.00	1.00	G	G	6	7
SP	34	92	0.96	0.98	G	G	3	3
SS	34	116	1.00	1.00	G	G	13	9
SU	55	106	1.00	1.00	G	G	3	3
TR	25	61	0.14	0.22	W	W	9	7
TT	43	45	0.20	0.36	W	W	3	3
VU	97	65	0.85	1.00	G	G	5	5
YT	50	80	0.02	0.48	W	W	10	10

Table S3.2. Number of follow hours (in hours) and cumulative distance moved (in km) used to estimate average speed of lion movement. Data was collected during 4-day continuous follows of individual Serengeti prides carried out between September 1984 and December 1987 (see Packer et al. 1990, Scheel & Packer 1991). Distance moved was derived from car odometer readings. For the purpose of this study, followed prides were assigned to woodland or grassland habitat based on the dominant habitat type within their 75% home range. Values associated with night-time periods are given in parentheses.

		Number of follow hours		Cumulative distance moved	
Habitat	Pride code	Dry season	Wet season	Dry season	Wet season
Woodland	KB	96 (48)	36 (14)	14.6 (12.2)	4.5 (3.6)
	CS	96 (36)	96 (36)	11.3 (9.9)	14.1 (10.4)
	LL	72 (30)	72 (24)	9.7 (8.9)	8.3 (7.6)
Grassland	SP	96 (48)	96 (48)	16.6 (13.8)	18.1 (14.7)
	PN	96 (48)	-	15.5 (13.0)	-
	SB	96 (48)	96 (48)	17.8 (14.6)	19.0 (15.4)
	SU	-	96 (48)	-	17.3 (14.1)

REFERENCES

Athreya, V., M. Odden, J. D. Linnell, J. Krishnaswamy, and U. Karanth (2013). Big cats in our backyards: persistence of large carnivores in a human dominated landscape in India. *PLoS One* **8**, e57872.

Bertram, B. C. (1975). Social factors influencing reproduction in wild lions. *Journal of Zoology* **177**, 463–482.

Borchers, D. L., and M. G. Efford (2008). Spatially explicit maximum likelihood methods for capture–recapture studies. *Biometrics* **64**, 377–385.

Bygott, J. D., B. C. Bertram, and J. P. Hanby (1979). Male lions in large coalitions gain reproductive advantages. *Nature* **282**, 839–841.

Calenge, C. (2006). The package adehabitat for the R software: a tool for the analysis of space and habitat use by animals. *Ecological Modelling* **197**, 516–519.

Carbone, C., S. Christie, K. Conforti, T. Coulson, N. Franklin, J. R. Ginsberg, M. Griffiths, J. Holden, K. Kawanishi, M. Kinnaird, R. Laidlaw, A. Lynam, D. W. Macdonald, D. Martyr, C. MacDougal, L. Nath, T. O'Brien, J. Seidensticker, D. J. L. Smith, M. Sunquist, R. Tilson, and W. N. Shahruddin (2001). The use of photographic rates to estimate densities of tigers and other cryptic mammals. *Animal Conservation* **4**, 75–79.

Chandler, R. B., and J. A. Royle (2013). Spatially explicit models for inference about density in unmarked or partially marked populations. *Annals of*

Applied Statistics **7**, 936–954.

Durant, S. M., M. E. Craft, R. Hilborn, S. Bashir, J. Hando, and L. Thomas (2011). Long-term trends in carnivore abundance using distance sampling in Serengeti National Park, Tanzania. *Journal of Applied Ecology* **48**, 1490–1500.

Foster, R. J., and B. J. Harmsen (2012). A critique of density estimation from camera trap data. *The Journal of Wildlife Management* **76**, 224–236.

Funston, P. J., L. Frank, T. Stephens, Z. Davidson, A. Loveridge, D. W. Macdonald, S. Durant, C. Packer, A. Mosser, and S. M. Ferreira (2010). Substrate and species constraints on the use of track incidences to estimate African large carnivore abundance. *Journal of Zoology* **281**, 56–65.

Gardner, B., J. Reppucci, M. Lucherini, and J. A. Royle (2010). Spatially explicit inference for open populations: estimating demographic parameters from camera-trap studies. *Ecology* **91**, 3376–3383.

Gopalaswamy, A. M., J. A. Royle, J. E. Hines, P. Singh, D. Jathanna, N. Kumar, and K. U. Karanth (2012). Program SPACECAP: software for estimating animal density using spatially explicit capture–recapture models. *Methods in Ecology and Evolution* **3**, 1067–1072.

Gray, T. N. E., and S. Prum (2012). Leopard density in post-conflict landscape, Cambodia: evidence from spatially-explicit capture-recapture. *The Journal of Wildlife Management* **76**, 163–169.

Groom, R. J., P. J. Funston, and R. Mandisodza (2014). Surveys of lions

Panthera leo in protected areas in Zimbabwe yield disturbing results: what is driving the population collapse? *Oryx* **48**, 385–393.

Grunblatt, J., W. K. Ottichilo, and R. K. Sinange (1989). A hierarchical approach to vegetation classification in Kenya. *African Journal of Ecology* **27**, 45–51.

Hopcraft, J. G. C., A. R. E. Sinclair, and C. Packer (2005). Planning for success: Serengeti lions seek prey accessibility rather than abundance. *Journal of Animal Ecology* **74**, 559–566.

Jennelle, C. S., M. C. Runge, and D. I. MacKenzie (2002). The use of photographic rates to estimate densities of tigers and other cryptic mammals: a comment on misleading conclusions. *Animal Conservation* **5**, 119–120.

Jones, J. P., G. P. Asner, S. H. Butchart, and K. U. Karanth (2013). The "why" "what" and "how" of monitoring for conservation. *Key Topics in Conservation Biology* **2**, 327–343.

Manzo, E., P. Bartolommei, J. M. Rowcliffe, and R. Cozzolino (2012). Estimation of population density of European pine marten in central Italy using camera trapping. *Acta Theriologica* **57**, 165–172.

Meek, P. D., P. J. S. Fleming, A. G. Ballard, P. B. Banks, A. W. Claridge, J. G. Sanderson, and D. E. Swann (2014). *Camera trapping: wildlife management and research.* CSIRO Publishing, Melbourne.

Mosser, A., J. M. Fryxell, L. Eberly, and C. Packer (2009). Serengeti real estate: density vs. fitness-based indicators of lion habitat quality. *Ecology*

Letters **12**, 1050–1060.

Mosser, A., and C. Packer (2009). Group territoriality and the benefits of sociality in the African lion, *Panthera leo*. *Animal Behaviour* **78**, 359–370.

Norton-Griffiths, M. (1975). The patterns of rainfall in the Serengeti ecosystem, Tanzania. *East African Wildlife Journal* **13**, 347–374.

O'Connell, A. F., J. D. Nichols, and K. U. Karanth (2010). *Camera traps in animal ecology: methods and analyses*. Springer, Tokyo.

Ogutu, J. O., H.-P. Piepho, H. T. Dublin, R. S. Reid, and N. Bhola (2006). Application of mark-recapture methods to lions: satisfying assumptions by using covariates to explain heterogeneity. *Journal of Zoology* **269**, 161–174.

Packer, C., R. Hilborn, A. Mosser, B. Kissui, M. Borner, G. Hopcraft, J. Wilmshurst, S. Mduma, and A. R. Sinclair (2005). Ecological change, group territoriality, and population dynamics in Serengeti lions. *Science* **307**, 390–393.

Packer, C., and A. E. Pusey (1993). Should a lion change its spots? *Nature* **362**, 595.

Packer, C., A. E. Pusey, and L. E. Eberly (2001). Egalitarianism in female African lions. *Science* **293**, 690–693.

Packer, C., D. Scheel, and A. E. Pusey (1990). Why lions form groups: food is not enough. *The American Naturalist* **136**, 1–19.

Reed, D. N., T. M. Anderson, J. Dempewolf, K. Metzger, and S. Serneels

(2009). The spatial distribution of vegetation types in the Serengeti ecosystem: the influence of rainfall and topographic relief on vegetation patch characteristics. *Journal of Biogeography* **36**, 770–782.

Riggio, J., A. Jacobson, L. Dollar, H. Bauer, M. Becker, A. Dickman, P. Funston, R. Groom, P. Henschel, H. de Iongh, L. Lichtenfeld, and S. Pimm (2013). The size of savannah Africa: a lion's (*Panthera leo*) view. *Biodiversity and Conservation* **22**, 17–35.

Rovero, F., and A. R. Marshall (2009). Camera trapping photographic rate as an index of density in forest ungulates. *Journal of Applied Ecology* **46**, 1011–1017.

Rovero, F., F. Zimmermann, D. Berzi, and P. Meek (2013). "Which camera trap type and how many do I need?" A review of camera features and study designs for a range of wildlife research applications. *Hystrix, the Italian Journal of Mammalogy* **24**, 148–156.

Rowcliffe, J. M., C. Carbone, P. A. Jansen, R. Kays, and B. Kranstauber (2011). Quantifying the sensitivity of camera traps: an adapted distance sampling approach. *Methods in Ecology and Evolution* **2**, 464–476.

Rowcliffe, J. M., C. Carbone, R. Kays, B. Kranstauber, and P. A. Jansen (2014). Density estimation using camera trap surveys: the random encounter model. In *Camera trapping: wildlife management and research*, pp. 317–324. CSIRO Publishing, Melbourne.

Rowcliffe, J. M., J. Field, S. T. Turvey, and C. Carbone (2008). Estimating animal density using camera traps without the need for individual recognition. *Journal of Applied Ecology* **45**, 1228–1236.

Rowcliffe, J. M., R. Kays, C. Carbone, and P. A. Jansen (2013). Clarifying assumptions behind the estimation of animal density from camera trap rates. *The Journal of Wildlife Management* **77**, 876–876.

Royle, J. A., J. D. Nichols, K. U. Karanth, and A. M. Gopalaswamy (2009). A hierarchical model for estimating density in camera-trap studies. *Journal of Applied Ecology* **46**, 118–127.

Schaller, G. B. (1972). *The Serengeti lion: a study of predator-prey relations*. University of Chicago Press, Chicago.

Scheel, D., and C. Packer (1991). Group hunting behaviour of lions: a search for cooperation. *Animal Behaviour* **41**, 697–709.

Seber, G. A. F. (1982). *The estimation of animal abundance and related parameters*. Macmillan, New York.

Silverman, B. W. (1986). *Density estimation*. Chapman and Hall, London.

Sinclair, A. R. E., S. A. R. Mduma, J. G. C. Hopcraft, J. M. Fryxell, R. Hilborn and S. Thirgood (2007). Long-term ecosystem dynamics in the Serengeti: lessons for conservation. *Conservation Biology* **21**, 580–590.

Sollmann, R., M. M. Furtado, B. Gardner, H. Hofer, A. T. A. Jacomo, N. M. Torres, and L. Silveira (2011). Improving density estimates for elusive carnivores: accounting for sex-specific detection and movements using spatial capture recapture models for jaguars in central Brazil. *Biological Conservation* **144**, 1017–1024.

Swanson, A., M. Kosmala, C. Lintott, R. Simpson, A. Smith, and C. Packer (2015). Snapshot Serengeti, high-frequency annotated camera trap images of 40 mammalian species in an African savanna. *Scientific data*, DOI: 10.1038/sdata.2015.26.

Thomas, L., S. T. Buckland, E. A. Rexstad, J. L. Laake, S. Strindberg, S. L Hedley, J. R. B. Bishop, T. A. Marques, and K. P. Burnham (2010). Distance software: design and analysis of distance sampling surveys for estimating population size. *Journal of Applied Ecology* **47**, 5–14.

Tobler, M. W., S. E. Carrillo-Percastegui, R. Leite Pitman, R. Mares, and G. Powell (2008). An evaluation of camera traps for inventorying large- and medium-sized terrestrial rainforest mammals. *Animal Conservation* **11**, 169–178.

Zero, V. H., S. R. Sundaresan, T. G. O'Brien, and M. F. Kinnaird (2013). Monitoring an endangered savannah ungulate, Grevy's zebra *Equus grevyi*: choosing a method for estimating population densities. *Oryx* **47**, 410–419.

Chapter 4

Revealing kleptoparasitic and predatory tendencies in an African mammal community using camera traps: a comparison of spatiotemporal approaches

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Revealing kleptoparasitic and predatory tendencies in an African mammal community using camera traps: a comparison of spatiotemporal approaches

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ABSTRACT

Camera trap data are increasingly being used to characterise relationships between the spatiotemporal activity patterns of sympatric mammal species, often with a view to inferring inter-specific interactions. In this context, we attempted to characterise the kleptoparasitic and predatory tendencies of spotted hyaenas (*Crocuta crocuta*) and lions (*Panthera leo*) from photographic data collected across 54 camera trap stations and two dry seasons in Tanzania's Ruaha National Park. We applied four different methods of quantifying spatiotemporal associations, including one strictly temporal approach (activity pattern overlap), one strictly spatial approach (co-occupancy modelling), and two spatiotemporal approaches (co-detection modelling and temporal spacing at shared camera trap sites). We expected a kleptoparasitic relationship between spotted hyaenas and lions to result in a positive spatiotemporal association, and further hypothesised that the association between lions and their favourite prey in Ruaha, the giraffe (*Giraffa camelopardalis*) and the zebra (*Equus quagga*), would be stronger than those observed with non-preferred prey species (the impala *Aepyceros melampus* and the dikdik *Madoqua kirkii*). Only approaches incorporating both the temporal and spatial components of camera trap data resulted in significant associative patterns. The latter were particularly sensitive to the temporal resolution chosen to define species detections (i.e. occasion length), and only revealed a significant positive association between lion on spotted hyaena detections, as well as a tendency for both species to follow each other at camera trap sites, during the dry season of 2013, but not that of 2014. In both seasons, observed spatiotemporal associations between lions and each of the four herbivore species considered provided no convincing or consistent indications of any predatory preferences. Our study suggests that, when making inferences on inter-specific interactions from camera trap data, due regards should be given to the potential behavioural and methodological processes underlying observed spatiotemporal patterns.

INTRODUCTION

With the advent of more affordable remote tracking and sensing technologies, researchers have turned to inferring likely interactive processes from the way animals distribute their activity in space and time (Latombe et al. 2013, Vanak et al. 2013, Potts et al. 2014). In particular, photographic data from remotely triggered camera traps are increasingly being used to characterize the spatiotemporal activity patterns of sympatric mammal species (Burton et al. 2015), as well as the potential relationships between them (Foster et al. 2013, Bischof et al. 2014, Lesmeister et al. 2015, Tambling et al. 2015). Such data have primarily been used to investigate instances of spatiotemporal niche partitioning between competing species, and sympatric carnivores in particular (Schuette et al. 2013, Kays et al. 2015, Sunarto et al. 2015). In contrast, few studies have aimed to quantify more direct interactions, such as kleptoparasitism and predation, which involve a degree of contact between individuals of different species.

Kleptoparasitic species and their victims can be expected to co-occur in space and time more than expected by chance, either because they converge at kill sites, or because the former harass or follow the latter (Brockmann and Barnard 1979). In contrast, predator-prey relationships may result in several spatiotemporal outcomes ranging from complete avoidance (i.e. outcome driven by predator avoidance) to complete overlap (i.e. outcome driven by predator attraction) (Sih 1984, Tilman and Kareiva 1997, Laundré et al. 2001, Broekhuis et al. 2013, Swanson et al. 2014). Thus, although kleptoparasitic behaviour may be characterized by a strong positive association, predatory tendencies may prove more challenging to measure unambiguously. Here, we test whether camera trap data can be used to quantify these tendencies in a multi-species system.

Camera trap surveys typically sample multiple species across a given landscape, with the resulting photographs providing information on when and where each one was detected (Rovero et al. 2013). A range of methods now exists to extract and compare spatial and/or temporal patterns for sympatric species from camera trap data, with a view to inferring interactive behaviours (Burton et al. 2015). Of these, strictly temporal approaches focus primarily on the timing of photographic events, which can be used to construct species-specific activity patterns (Rowcliffe et al. 2014). The resulting distributions are typically compared across species and a measure of temporal overlap estimated from them (Linkie and Ridout 2011). Importantly, such approaches tend to disregard the spatial component of camera trap data. In contrast, strictly spatial approaches assess the absolute or relative use of camera trap locations by different species, and investigate whether or not these are correlated. In recent years, occupancy models that account for imperfect detection (i.e. a species goes undetected at a site where it is present) have become a popular tool to achieve this (Mackenzie et al. 2002, Burton et al. 2015). Such models allow for the inclusion of site and observation covariates, which are thought to be informative of the spatial and temporal heterogeneity in species occurrence and detection, respectively (Mackenzie et al. 2002). Moreover, multi-species occupancy models now allow for estimates of site co-occupancy to be obtained between pairs or groups of species (Mackenzie et al. 2004, Waddle et al. 2010).

Photographic data collected using camera trap grids rarely satisfy the basic assumptions of the occupancy-modelling framework (Miller et al. 2015). The area sampled by each individual camera trap is neither closed to changes in the occupancy state of most photographed animals, nor spatially independent from other sites within the deployed grid. These assumptions are especially problematic for wide-ranging mammals (Efford and Dawson 2012), leading to biased or imprecise estimates of occupancy, and by extension co-occupancy. Furthermore, the estimation of detection probability, which is used to correct for false absences, requires continuous camera trap surveys to be discretized into an arbitrary number of sampling occasions, the length of which can vary considerably from one study to another, e.g. from 1 to as many as 15 consecutive days (Linkie et al. 2007, Thorn et al. 2009). Choice of occasion length may also influence estimates of co-occupancy, yet this aspect of occupancy modelling as applied to camera trap data has so far received little attention.

Most importantly, the estimation of spatial or temporal co-occurrence often requires observations to be integrated over either large temporal or spatial scales, respectively. For example, patterns of co-occupancy are often estimated from data collected over several months (Robinson et al. 2014). So-called static measures of interaction ignore the dynamic nature of most interactive behaviour (Long et al. 2014). For instance, a predator and its prey may share the same spatial distribution, but use areas at different times (Courbin et al. 2013, Latombe et al. 2013). In this case, focusing on the detection process, that is, estimating the probability of detecting two species at the same site and point in time, may yield associations that are more representative of the interactive processes at hand. As for co-occupancy, however, estimates of co-detection may be influenced by choice of occasion length.

In this study, we apply four different methods of quantifying spatiotemporal associations between species to camera trap data collected on medium to large terrestrial mammals in Tanzania's Ruaha landscape (Table 4.1). Specifically, we apply one strictly temporal approach (activity pattern overlap), one strictly spatial approach (co-occupancy modelling), and two spatiotemporal approaches (co-detection modelling and temporal spacing at shared camera trap sites) to describe spatiotemporal associations between spotted hyaena (*Crocuta crocuta*) and lions (*Panthera leo*), as well as between lions and four herbivore species. Importantly, when implementing co-occupancy and co-detection models, we test a range of occasion lengths and assess the consistency in resulting spatial and spatiotemporal associations, respectively. Spotted hyaenas and lions are well known for stealing each other's kills (Kruuk 1972, Höner et al. 2002), and we thus expected a positive spatiotemporal association between the two species. In contrast, predator-herbivore interactions could result in one of three types of association: positive (i.e. dominated by attraction to prey), negative (i.e. dominated by predator avoidance), and random. Giraffes (*Giraffa camelopardalis*) and zebras (*Equus quagga*) are both preferred prey of lions (Hayward and Kerley 2005), and in Ruaha are frequently recorded at kill sites (Muneza et al. 2016; A. J. Dickman, unpublished data). We thus expected associations between lions and these two herbivore species to be either significantly negative or positive. In contrast, we expected lions to demonstrate random spatiotemporal associations with impala (*Aepyceros melampus*) and dikdik (*Madoqua kirkii*), which are not within the preferred prey body size range put forward by Hayward and Kerley (2005).

Table 4.1. Overview of the spatiotemporal approaches implemented in this study.

Method	Description
Activity pattern overlap	Qualitative assessment of the degree of temporal overlap between the activity patterns of two species
Co-occupancy modelling	Quantitative assessment of the influence of one species' occupancy on the occupancy of another, both corrected for imperfect detection
Co-detection modelling	Quantitative assessment of the influence of one species' binary detection/non-detection on the binary detection/non-detection of another
Temporal spacing	Quantitative assessment of the temporal spacing between successive detections of two species at shared camera trap sites

METHODS

Study area

The study was carried out on the eastern side of Ruaha National Park (RNP) in southern-central Tanzania (Figure 4.1). RNP is Tanzania's largest national park, encompassing an area of 20,226 km^2, and supports a diverse community of mammal species, including a full guild of large carnivores (Abade et al. 2014, Cusack et al. 2015a). The climate of RNP is semi-arid, with rainfall peaks occurring from December to January and March to April, and an average annual rainfall of 500 mm (Stolberger 2012). Altitude across the landscape ranges from 696 to 2171 m asl. The vegetation cover is a mosaic of typical East African semi-arid savannah and northerly Zambesian miombo woodland, including *Acacia*, *Combretum* and *Commiphora* species (Stolberger 2012). The Great Ruaha River, which runs along the south-eastern boundary of RNP, is the main water supply in the study area, providing a key resource for most wildlife during the dry season from June to November. Our study focuses on an area of approximately 120 km^2 situated close to the park headquarters (Figure 4.1).

Camera trap survey

The study area was first divided into 2-km^2 grid cells in Quantum GIS 2.6.0 (QGIS Development Team, http://qgis.org), following standardized multi-species camera trapping protocols (Ahumada et al. 2011). Fifty-four adjacent cells were then selected randomly to make up a continuous camera trap array (Figure 4.1). Approximate camera trap location within each cell was chosen randomly and located in the field using a handheld GPS device (Garmin Etrex 10, Garmin International, Inc., Olathe, Kansas, USA). Actual placement was on the closest natural game trail within 50 m of the random point. Game trails were defined as a continuous, grassless route through the habitat measuring at least 1 m in width and showing clear evidence of current usage by wild animals (e.g. presence of fresh droppings, spoor, or recently flattened grass either side of the trail). Within this study area, camera trap placement on natural game trails has been shown to increase detection of large carnivore species relative to random camera placements, but not that of herbivore prey (Cusack et al. 2015a). We did not use baits or lures to increase detection rates of carnivore species. All camera traps (Reconyx HC500, Reconyx, Inc., Holmen, Wisconsin, USA) were placed on trees at a height of 0.3 m off the ground, and positioned between 3 and 5 meters away from, and at an angle to, the game trail to ensure adequate detection of faster moving animals. Cameras were set to take five successive photos per trigger with no delay between consecutive triggers. The date and time were automatically stamped onto each image. Vegetation was cleared for a few meters in front of each camera but not otherwise disturbed. Altitude across camera locations ranged from 801 to 956 m.

At each camera trap location, we recorded characteristics of the habitat that were then used as covariates in relevant modelling frameworks (see below). These included the density of trees and shrubs (the number of live standing trees and shrubs within a radius of 50 m centred on the camera trap) and the distance to the nearest permanent body of water, which was derived from QGIS layers. Site-specific relative prey abundances for lions and spotted hyaenas were calculated from the camera trap data. Prey species for each carnivore were selected within the preferred prey body mass range (Hayward and Kerley 2005, Hayward 2006; Table S4.1). Relative prey abundance was interpreted as an index of prey encounter rate (PER), defined as the number of independent camera records (> 1 hour interval) divided by the number of days the camera location was active, and multiplied by 100 (i.e. events per 100 camera trap days, see Carbone et al. 2001). We do not interpret PER as an index of abundance, but rather as the likelihood for a carnivore to encounter an herbivore within the space surveyed by the camera trap. Camera trap data were collected for three months (Sep-Nov) in the dry seasons of 2013 and 2014 as part of a multi-species survey (Cusack et al. 2015a).

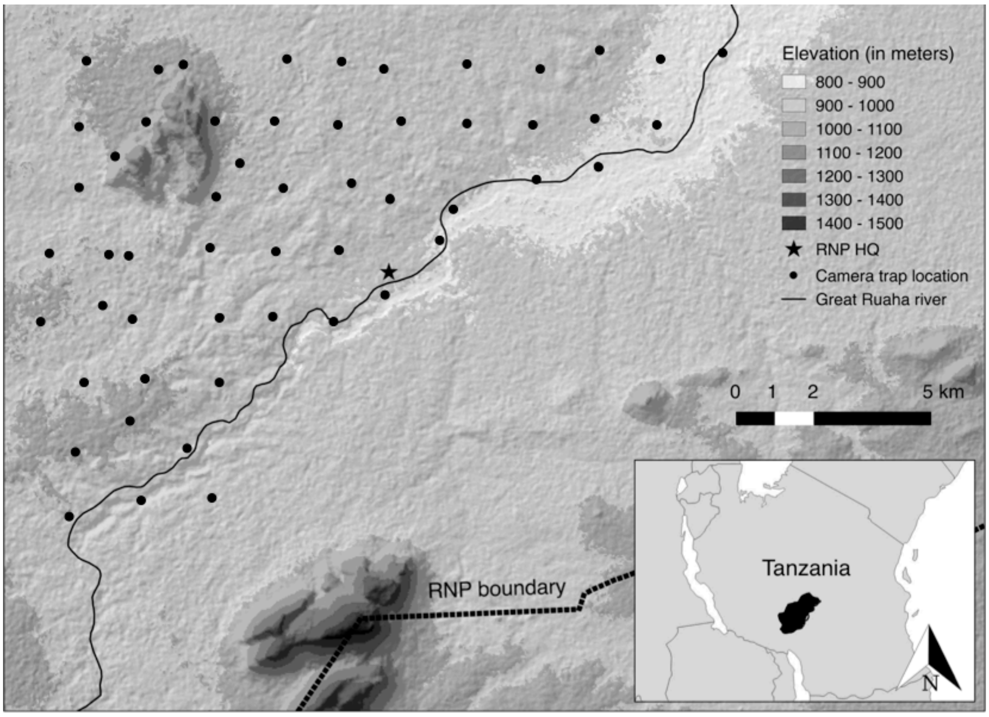

Figure 4.1. Location of camera trap sites within Ruaha National Park (RNP). The inset map shows the location of RNP in southern-central Tanzania.

Only a subset of the wider mammal community found in RNP was considered (Cusack et al. 2015a). Specifically, we considered two species of large carnivore – the lion and the spotted hyaena – that are known to co-occur in the study landscape, and four species of herbivore, namely the dikdik, the impala, the zebra and the giraffe. These species were selected to represent a range of herbivore body sizes, and included two preferred (giraffe and zebra) and two non-preferred species (impala and dikdik) (Hayward and Kerley 2005). These species were also commonly photographed and thus ensured adequate sample sizes for all analyses.

Activity pattern overlap

The coefficient of overlap (Δ), implemented in the overlap package in R, was used to estimate temporal overlap between species activity patterns (Ridout and Linkie 2009, Meredith and Ridout 2014). This approach illustrated the process of aggregating spatial observations to compare the activity of species over 24 hours. As suggested by Meredith and Ridout (2014), the non-parametric estimator Δ_1 was used for all species comparisons as sample sizes for lions tended to be lower than 50 photographic events per season. We expected relatively high levels of overlap between the activity patterns of lions and spotted hyaenas, as well as between those of lions and both zebra and giraffes. To account for the primarily nocturnal behaviour of predators, we further investigated correlations between species-specific counts of photographic events obtained during each night hour (18h00 to 06h00). We expected to find significant positive relationships between the hourly counts of spotted hyaenas and lions, as well as between those of lions and both zebra and giraffes.

Co-occupancy modelling

To test for spatial associations between species, we implemented a Bayesian multi-species occupancy-modelling framework (Waddle et al. 2010). The latter models hierarchical interactions between co-occurring species, each of these identified as being either dominant (i.e. having an effect on another species) and/or subordinate (i.e. being affected by another species). The resulting parameterization improved covariate fitting and allowed for more complex models to be fitted despite wide variations in sample sizes for different species (Waddle et al. 2010). Co-occupancy models retain the basic assumptions of the general occupancy framework (Mackenzie et al. 2002), namely 1) that sites are closed to changes in the occupancy status of the target species, 2) that sites and occasions are spatially and temporally independent, respectively, and 3) that there remains no un-modelled heterogeneity in both occupancy and detection. For the purpose of this study, we relaxed these assumptions by interpreting probability of site occupancy as the probability of site use (assumption 1), an approach that has been used in the past to address lack of spatial independence between sampling sites (see recommendations by Mackenzie 2006). We also acknowledge that arbitrary choice of occasion length may result in some temporal dependence (assumption 2), and admit that the inclusion of covariates on occupancy and detection represented a compromise between model complexity and interpretability (assumption 3). Hereafter, we use the term "occupancy" to describe the probability of camera site use.

For each of the six species considered, separate detection matrices were constructed based on occasion lengths of one, five and 10 days. In all matrices, a 1 signified the species had been photographed at least once at a given camera location on a given occasion whilst a 0 signified it had not. Spatial associations were assessed between lions and spotted hyaenas, as well as between lions and each herbivore species, whilst controlling for environmental factors influencing species-specific occupancy and detection. For each dry season and occasion length, two co-occupancy models were considered. In the first, all herbivore occupancies affected lion occupancy, which in turn affected spotted hyaena occupancy. The second model was identical to the first except that spotted hyaena occupancy affected lion occupancy, instead of the reverse. We chose to implement these two models to account for uncertainty regarding the nature of the kleptoparasitic relationship between lions and spotted hyaenas (Kruuk 1972, Höner 2002). For both of these species, PER was used to control for the effect of prey availability on both occupancy and detection, whilst distance to water was included as a covariate for occupancy only. Lions have been shown to hunt in areas of higher prey accessibility (i.e. better vegetation cover) rather than abundance (Hopcraft et al. 2005), and vegetation cover was therefore included as a covariate on lion occupancy. Predator-herbivore interactions were modelled as the effect of each herbivore species on lion occupancy. We did not consider the reverse effect of lions on herbivore occupancy (i.e. predator avoidance), but instead assumed that a negative effect of prey on predator could be due to a tendency for the former to avoid the latter. For all herbivore species, distance to water and vegetation cover were included as covariates for occupancy. In addition, distance to water was also added as a covariate for detection since herds in the study area were observed to remain by the river for several days before moving inland.

Parameters describing inter-specific effects were considered to be significant if the 95% credible interval of the posterior distribution mean did not include zero (Gelman and Rubin 1992). Models were implemented using the R2jags (Su and Yajima 2012) and rjags (Plummer 2014) packages in R (R Development Core Team 2014). We used uniform priors defined on the log-odds interval [-10,10] for all parameter distributions and ran models with 3 chains of 30,000 iterations, including 10,000 iteration burn-ins. Convergence was assessed from both the R-hat value (<1.1 for reliable convergence) and visual inspection of chain trace plots (Gelman and Rubin 1992).

Co-detection modelling

We modelled the probability of detecting lions and spotted hyaenas at a given camera site on a given occasion (binary response variable) as a function of inter-specific effects using binomial mixed-effects models (Bolker et al. 2009). As for co-occupancy, we tested models based on occasion lengths of one, five and 10 days. This approach was analogous to the estimation of inter-specific effects on detection probability in an occupancy framework; only here detection represented the ecological process of interest, rather than a correction for false negative observations (Mackenzie et al. 2002). Lion detection was modelled as a function of five binary explanatory variables consisting of the separate detection/non-detection of dikdiks, impalas, zebras and giraffes, as well as that of spotted hyaenas. For spotted hyaenas, inter-specific effects consisted of two binary variables: the detection/non-detection of lions and that of any known prey species (Table S4.1). In all models, camera site ID was fitted as a random intercept to control for the influence of camera-related factors (e.g. distance to water, vegetation cover). Occasions when a camera was inactive were excluded from the analysis. Models were implemented using the R package lme4 (Bolker et al. 2009). P-values for estimated coefficients were derived using an approximation of the Wald statistic, defined as the coefficient estimate divided by its standard error.

Temporal spacing of detections at shared camera sites

For each site at which two species were observed to co-occur, we determined the number of hours separating the detection of one species (hereafter, reference detection) and the next detection of the other species (hereafter, follow-up detection). If the reference detection was followed by another detection of the same species, it was excluded from the analysis. From the resulting values we derived the empirical probability distribution of detecting spotted hyaenas, as well as all four herbivores, for the first time during days one to 10 before and after detection of a lion at the same camera trap. For each day (n = 20), probabilities were obtained by dividing the number of follow-up detections falling into that day by the total number of detections for the corresponding species. Graphically, we obtained a distribution of detection probabilities for 10 days before (i.e. the probability for a lion to "follow" one of the other species at the same camera trap) and after (i.e. the probability for one of the other species to "follow" lions) detection of a lion at time 0. We considered follow-up detections occurring within 10 days of reference detections to match occasion length choice in co-occupancy and co-detection approaches. We further assumed that interactive processes were unlikely to play out over longer time periods.

To test whether observed detection probabilities were more or less than expected if the temporal spacing between detections of two species at shared camera traps was random, we randomised the timing of detections of the follow-up species 1000 times to generate expected distributions for each day. Each iteration of the randomisation procedure implemented the following steps for every detection of the follow-up species: 1) a new date was selected at random from the period of activity of the corresponding camera trap; 2) a new time was selected by sampling the activity pattern probability density function for the corresponding species; 3) the number of hours separating the randomised follow-up detections and the unchanged references ones was derived. This resulted in 1000 expected values of detection probability for each day (10 days before and after a lion detection), which we compared to the observed value using a standard permutation test. The latter computed the two-tailed probability $P = (n_e + 1)/N$ of getting a value that was more or less than the observed level, where N is the total number expected values and n_e is the number of values lesser or greater than the observed. All statistical tests were performed based a significance level of $\alpha = 0.05$. Data used in this study are available from Cusack et al. (2015b).

RESULTS

We implemented 3,616 and 3,643 camera trap days in the dry seasons of 2013 and 2014, respectively. In both seasons, the spotted hyaena and the impala were the most photographed large carnivore and herbivore species, respectively. The lion was the least photographed carnivore in both seasons, whilst the dikdik and the zebra were the least photographed herbivore species in 2013 and 2014, respectively (Table 4.2). Naïve occupancy, defined as the proportion of sites where a target species was detected, ranged from 0.442 (lion) to 1 (impala) in the dry season of 2013 and from 0.419 (dikdik) to 0.930 (impala) in 2014. Naïve detection, defined as the proportion of camera trap days on which a target species was detected, was low for most species, ranging from 0.012 to 0.280 in 2013 and from 0.010 to 0.283 in 2014 (both lion and impala, respectively) (Table 4.2). A full list of photographed species can be found in Cusack et al. (2015a).

Activity pattern overlap

Activity pattern overlap between lions and spotted hyaenas was high in both dry seasons considered (Table 4.3, Figure S4.1). Temporal overlap between lions and each herbivore species varied noticeably, with highest and lowest overlap found with dikdiks and giraffes in both seasons, respectively. For all pairs of species considered, we found no significant relationships between counts of photographic events obtained during each night hour (Pearson product moment correlations: all P-values > 0.05).

Co-occupancy modelling

Parameter estimation in all multi-species models converged, with R-hat values consistently smaller than 1.05. Although we focus on posterior distributions associated with parameters describing inter-specific effects on occupancy, posterior distributions associated with environmental covariates on occupancy and detection for each species can be found in Tables S4.2 and S4.3. None of the inter-specific effects tested were found to be significant, although some did show a tendency to be either positive or negative. In particular, the effect of lions on spotted hyaena occupancy showed a negative tendency in the dry season of 2014, whilst the reverse effect of hyaenas on lion occupancy tended to be positive (Fig. 4.2a). Dikdiks and impalas did not appear to have any notable effect on lion occupancy (Fig. 4.2b and c). Whilst giraffe occupancy showed a slight tendency to positively influence that of lions in both seasons (Fig. 4.2e), the effect of zebra was negligible and appeared to vary in direction (Fig. 4.2d). Choice of occasion length did not appear to influence the estimation of inter-specific effects during the dry season of 2014. Differences between posterior distributions were more noticeable during the dry season of 2013, and particularly for the effect of lions on spotted hyaenas and that of dikdiks on lions. In these cases, increasing the length of occasions tended to result in posterior distributions that were less precise (i.e. more diffuse).

Table 4.2. Number of independent photographic events, naïve occupancy and naïve detection probabilities for two large carnivores (lion and spotted hyaena) and four herbivore species (dikdik, impala, zebra and giraffe) camera-trapped in Ruaha National Park, southern Tanzania. Photographic events occurring at the same site were judged to be independent if they were separated by more than 1 hour. Naïve occupancy and detection were calculated from detection matrices consisting of 54 rows (camera trap sites) and 90, 1-day occasions, and represent the proportion of sites where the species was detected at least once and the proportion of surveys (one camera trap day) on which the species was detected, respectively.

Taxonomic group	Latin name	Common name	Mass (kg)[a]	# photographic events		Naïve occupancy		Naïve detection	
				2013	2014	2013	2014	2013	2014
Carnivora	*Panthera leo*	Lion	161.5	50	43	0.442	0.442	0.012	0.010
	Crocuta crocuta	Spotted hyaena	63	303	300	0.791	0.814	0.058	0.065
Ungulata	*Madoqua kirkii*	Kirk's dikdik	5.3	170	280	0.535	0.419	0.039	0.058
	Aepyceros melampus	Impala	52.5	2207	2307	1.000	0.930	0.280	0.263
	Equus quagga	Zebra	400	191	194	0.651	0.674	0.047	0.048
	Giraffa camelopardalis	Giraffe	900	408	434	0.861	0.954	0.087	0.093

[a] Based on Smith et al. (2003).

Table 4.3. Estimated coefficient of temporal overlap with lions and associated 95% confidence interval (square parentheses).

	Coefficient of temporal overlap with lion	
Species	Dry season 2013	Dry season 2014
Spotted hyaena	0.75 [0.62 - 0.85]	0.70 [0.66 - 0.87]
Dikdik	0.63 [0.46 - 0.72]	0.62 [0.49 - 0.70]
Impala	0.29 [0.19 - 0.36]	0.46 [0.36 - 0.56]
Zebra	0.43 [0.35 – 0.52]	0.47 [0.36 – 0.59]
Giraffe	0.25 [0.18 - 0.34]	0.42 [0.50 - 0.33]

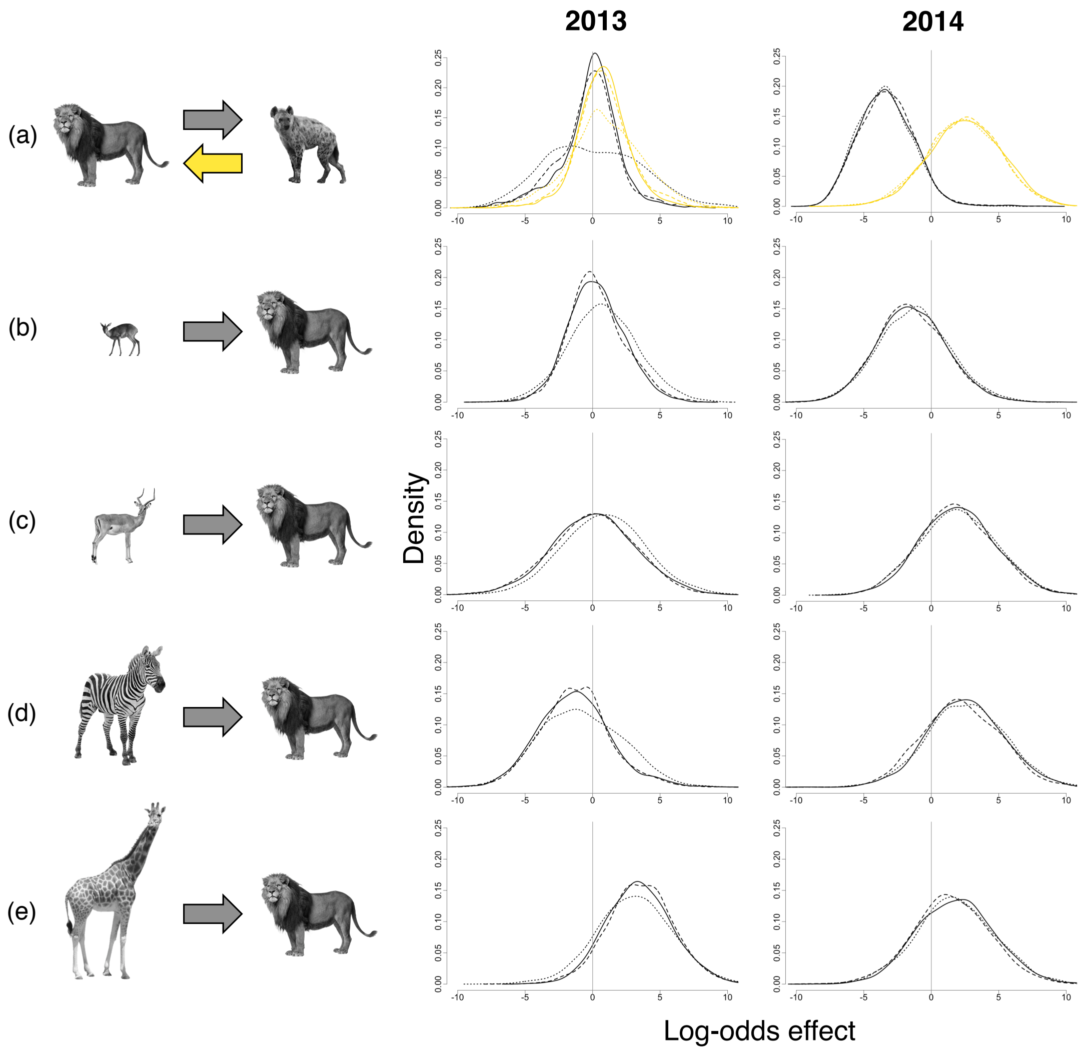

Figure 4.2. Posterior probability density functions associated with inter-specific effects on probability of occupancy for the dry seasons of 2013 and 2014, as estimated from hierarchical multi-species occupancy models. Occupancy is interpreted as the probability of camera trap site use by a species. Spatial associations consisted of the effect of lions and spotted hyaenas on each other's occupancy (**a**), and the effect of dikdiks, impala, zebras and giraffes on lion occupancy (**b**, **c**, **d** and **e**, respectively). Occasion lengths, which denote the temporal resolution of the species detection matrices, consist of one, five and 10 days, and are denoted by solid, dashed and dotted lines, respectively.

Co-detection models

In contrast to co-occupancy patterns, the direction and strength of inter-specific effects on the probability of detecting lions and spotted hyaenas at a given camera site on a given occasion was highly sensitive to choice of occasion length (Figure 4.3, Table S4.4). Based on an occasion length of one day, lions and hyaenas positively influenced each other's detection probability during the dry season of 2013, but not that of 2014. Only dikdik detection during the dry season of 2014 appeared to significantly influence the probability of detecting lions (Fig. 4.3). When an occasion length of five days was used, spotted hyaena detection was positively influenced by prey detection during the dry season of 2013, and by lion detection during 2014. Lion detection was positively influenced by spotted hyaena, impala and giraffe detections during the dry season of 2013, but only spotted hyaena detection in 2014. When an occasion length of 10 days was used, spotted hyaena detection was still found to positively influence that of lions during the dry season of 2013, whilst prey species detection positively influenced the probability of detecting spotted hyaenas during the dry season of 2014.

Temporal spacing of detections at shared camera sites

We did not estimate temporal spacing patterns for dikdiks and zebras, as sample sizes for both species were too small to construct reliable probability distributions. Spotted hyaenas were more likely to be detected within one day of a lion detection during the dry season of 2013 (Figure 4.4; observed = 0.030, expected = 0.016, $P < 0.05$), but showed no bias during the dry season of 2014 (observed = 0.010, expected = 0.014, $P = 0.624$). Detection probability for lions was only significantly higher than expected between one and two days following detection of a spotted hyaena (observed = 0.020, expected = 0.008, P

< 0.05). Impalas showed a tendency to be detected less often than expected by chance within one day of a lion detection, a pattern that was only significant during the dry season of 2014 (observed = 0.007, expected = 0.010, $P < 0.05$). Lastly, giraffes and lions did not appear to respond to each other's detections at shared camera traps, although giraffes did show a tendency to be detected more than expected by chance between seven and eight days before and after a lion detection (Figure 4.4).

DISCUSSION

We were interested in assessing whether data collected from a standard camera trap grid could be used to characterise kleptoparasitic and predatory tendencies in an east African savannah ecosystem. Overall, we found that inferences regarding the kleptoparasitic relationship between lions and spotted hyaenas, and the predatory tendencies of lions in Ruaha National Park were dependent on both the approach used to quantify associations and the dry season in which the camera trap survey had been carried out. Specifically, of the four methods tested, only those incorporating both the temporal and spatial components of camera trap data (i.e. co-detection modelling and temporal spacing at shared camera traps) resulted in significant associative patterns from which inferences could be drawn. These inferences, however, were inconsistent across the two dry seasons considered, a finding that could either be explained by seasonal shifts in kleptoparasitic and predatory tendencies, or be indicative of the failure of our camera trap survey to consistently detect meaningful spatiotemporal patterns.

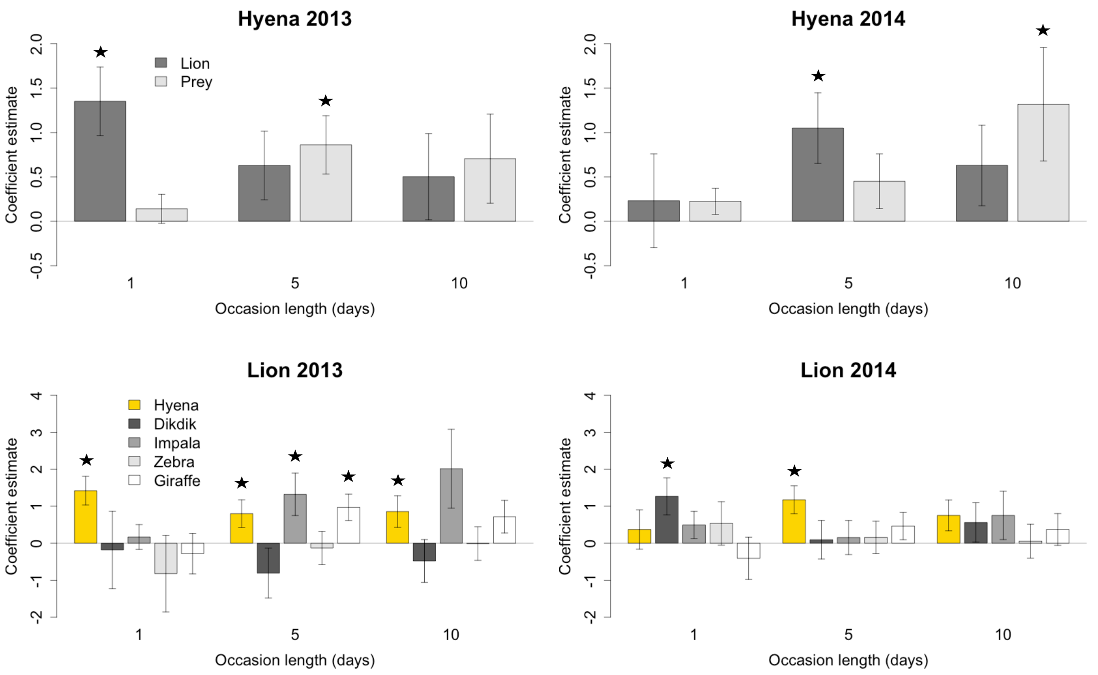

Figure 4.3. Coefficient estimates and associated standard errors for inter-specific effects on spotted hyaena (top row) and lion (bottom row) detection during the dry seasons of 2013 and 2014. Here, detection is a binary variable describing whether or not the target species was photographed at a given camera trap on a given occasion. Estimates were obtained from binomial mixed-effects models, which were parameterized using data from two dry seasons (2013 and 2014), arranged according to three different occasion lengths (one, five and 10 days). In all models, camera trap site ID was fitted as a random intercept. Estimates are given on the logit scale, with stars indicating significant effects. Significance was assessed using an approximation of the Wald statistic, defined as the coefficient estimate divided by its standard error. Note y-axes vary.

The direction of the kleptoparasitic relationship between lions and spotted hyaenas has proved difficult to generalise across locations in east and southern Africa (Périquet et al. 2015). Although spotted hyaenas are efficient hunters, killing up to 95% of their prey (Cooper et al. 1999), they will also readily kleptoparasitise carcasses from other predators, including lions (Kruuk 1972, Höner et al. 2002, Watts and Holekamp 2008). The latter species has also been found to scavenge from spotted hyaena kills (Kruuk 1972, Trinkel and Katsberger 2005). Indeed, Kruuk (1972) showed that more than 90 % of kills at which both species were encountered were hunted by hyaenas. In this context, there are currently no published studies documenting the kleptoparasitic behaviour of lions and spotted hyaenas in the Ruaha landscape of Tanzania. Our study suggests that both species do respond to each other's occurrence in space and time more than expected by chance, thus indicating the potential for kleptoparasitism. Although this was particularly the case for spotted hyaena during the dry season of 2013, lions did also show a tendency to follow hyaenas in 2014, albeit less markedly. Thus, our analysis of temporal spacing do not allow us to infer on the direction of this potential behaviour, since both species were found to follow each other at shared camera trap sites.

Interestingly, significant spatiotemporal associations between lions and hyaenas were largely absent during the dry season of 2014. This seasonal difference may reflect variation in the level of scavenging displayed by both species (Kruuk 1972), which has been linked to prey availability in past studies (Cooper 1999). However, the fact that prey detection was found to have no significant effect on spotted hyaena detection in 2014 (based on occasion lengths of one and five days), and that lion detection was unaffected by larger prey species, does not lend support to this hypothesis. Alternatively, the observed difference between the two dry seasons may reflect the inherent sampling error associated with our camera trap survey. Indeed, camera trap arrays typically sample a very small fraction of any given study landscape, and thus it is not surprising that interactive behaviours involving highly mobile species go undetected. Furthermore, we did not consider the influence of false negative detections (i.e. a camera fails to trigger as an animal passes in front of it), which could also have contributed towards increasing this sampling error. Thus, more detailed observational studies are needed to elucidate the extent of kleptoparasitism between lions and spotted hyaenas in RNP.

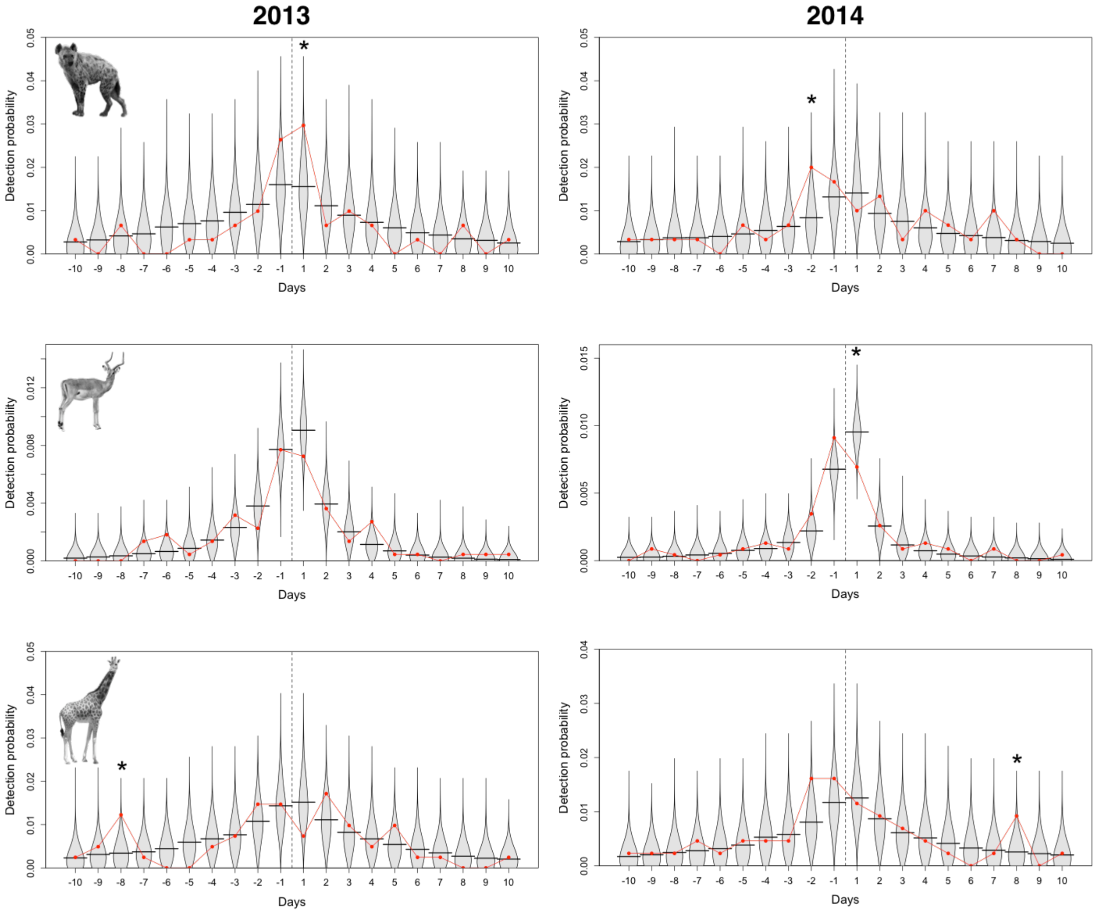

Figure 4.4. Observed (red) and expected (grey) distributions describing the probability of detecting spotted hyaenas, impala and giraffes for the first time during one to 10 days before and after detection of a lion at the same camera trap. For each day, detection probabilities were obtained by dividing the number of follow-up detections (i.e. photographic events of spotted hyaena, impala or giraffe) falling into that day by the total number of detections for the corresponding species. Grey bean plots represent expected distributions derived from 1000 randomisations of follow-up detections. Asterisks mark days for which observed detection probability was significantly different to expected.

In contrast, associations between lions and each of the four herbivore species considered provided no convincing indications of any predatory preferences. Contrary to expectations, co-detection models based on an occasion length of one day showed a positive effect of dikdik detection on lion detection during the dry season of 2014, despite this species not being actively sought by lions (Hayward and Kerley 2005). Similarly, impalas appeared to avoid using camera trap sites that had detected lions within the past 24 hours. Most importantly, more likely prey species, such as zebra and giraffe, were found to have no significant effect on lion occupancy and detection, regardless of the dry season. The latter finding may not be so surprising given that predator-prey spatiotemporal associations are typically the result of two simultaneous processes: attraction by the predator and avoidance by prey (Sih 1984). It is therefore possible that these two processes inhibited each other, thereby causing an absence of spatiotemporal association despite the existence of an interaction. Thus, more focused monitoring methods, such as direct observation, GPS collars, or scat analyses may be required to reliably elucidate predatory tendencies.

A number of factors may have contributed to the observed lack of distinctive patterns arising from the use of strictly spatial or temporal methods (i.e. activity pattern overlap and co-occupancy modelling). Firstly, our study was characterized by relatively high values of naive occupancy for most species considered, ranging across seasons from 0.44 to 0.81 for carnivores and from 0.52 to 1 for herbivores. These conservative values are reflective of the homogenous use of the study landscape by these species, which, in addition to the limited size of our camera trap grid, could have restricted the amount of information available to characterize patterns of spatial co-occurrence. A higher density of cameras than that implemented in this study may be needed to reliably portray fine-scale spatial associations (Waddle et al. 2010, Bischof et al. 2014). Secondly, the presence of the Great Ruaha River along one side of our camera trap grid – a huge draw for prey in the dry season – may have confounded patterns obtained from co-occupancy models; that is, lions and the three herbivore species may have found themselves in the same area for the sole reason of gaining access to water. We also note that distance to river did not seem to influence the probability of site use by either carnivores or herbivores. This suggests our grid may not have covered a large enough area to sample the resulting variation in space use, or that site use estimated over three months may have been confounded by the movement of animals towards and away from the river occurring over shorter time frames (e.g. during the day and at night, respectively).

In a similar way, patterns of temporal overlap are likely to have been confounded by the primarily nocturnal behaviour of lions, spotted hyaenas and dikdiks, which all showed high overlap in their activity patterns (Hayward and Hayward 2007). In contrast, temporal overlap was low between lions and giraffes owing to contrasting nocturnal and diurnal behaviours, respectively. Nonetheless, predator-prey relationships have been shown to occur despite limited temporal overlap. For example, most predation events of agoutis by ocelots were found to occur at the boundaries of both species' activity periods (Suselbeek et al. 2014). In the case of lions, zebras and giraffes, crepuscular hours may represent such a boundary (Hayward and Slotow 2009). More generally, however, qualitative assessment of the level of temporal overlap between species may only be useful when compared across different areas, each differing in their species composition (Ross et al. 2013, Tambling et al. 2015), thus allowing shifts in temporal activity to be more clearly attributed to interactive processes.

From a practical standpoint, very rarely will a camera trap survey yield sufficient detections of a species to allow occasion length to be shorter than 24 hours. On the contrary, occasion length is typically lengthened to increase species detection probability, and in turn the accuracy and precision of parameter estimates (Guillera-Arroita et al. 2010). Our study suggests this may be problematic when assessing spatiotemporal relationships between multiple species. Unlike co-occupancy estimates, co-detection models were highly sensitive to the level of temporal aggregation used to construct detection matrices. For example, while both lion and prey detection had seemingly no effect on spotted hyaena detection during the dry season of 2014 when an occasion length of one day was used, their importance changed considerably when occasion length was increased. Spatiotemporal associations between lions and herbivores were equally sensitive to occasion length, with the effect of each herbivore species varying substantially in both direction and strength across occasion lengths. Nevertheless, even an occasion length of one day is likely to be unsuitable for detecting behavioural patterns that have been shown to occur over time frames of a few hours. Courbin et al. (2015) recently showed that zebras fled from areas in which they had encountered lions within two hours of the encounter happening. Such a response is likely to go undetected by camera traps, unless these are deployed at a very high density. The cost of deploying more cameras, however, may surpass that of fitting GPS-collars to a subset of individuals, from which higher resolution spatiotemporal data may be obtained. If camera traps are to be used, we advise caution when defining what constitutes an occasion and recommend the development and application of more continuous ways of measuring detection probability (Guillera-Arroita et al. 2011).

Lastly, it is important to emphasise that the inter-specific interactions considered in this study have been under extensive investigation in numerous savannah ecosystems of east and southern Africa (Kruuk 1972, Schaller 1973, Hayward and Kerley 2005). As a result, our interpretation of observed spatiotemporal associations was based on some prior knowledge of the possible underlying processes. Had this not been the case, it is highly unlikely that any of the observed patterns would have been considered as conclusive evidence for kleptoparasitic and predatory tendencies. Camera traps have received considerable attention as a cost-effective way of studying inter-specific interactions in less well-known systems harbouring rare or elusive species, such as tropical forests or mountainous landscapes (Bischof et al. 2014, Alexander et al. 2015, Sunarto et al. 2015). However, our study suggests that in order to ensure robust inferences are drawn from such studies, due regards should be given to the potential behavioural and methodological processes underlying observed spatiotemporal patterns.

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SUPPORTING INFORMATION

Table S4.1. Identity and average body mass of herbivore prey species used to calculate an index of prey encounter rate.

Table S4.2. Mean and standard deviation for posterior distributions associated with environmental effects on probability of camera site occupancy.

Table S4.3. Mean and standard deviation for posterior distributions associated with environmental effects on probability of detection.

Table S4.4. Co-detection model estimates and standard errors.

Figure S4.1. Activity pattern overlap plots.

Table S4.1. Identity and average body mass of herbivore prey species used to calculate an index of prey encounter rate (PER) for lions and spotted hyenas from camera trap data collected in Ruaha National Park, southern Tanzania. Prey species for each carnivore were selected within the preferred prey body mass range.

Prey species[a]	Mass (kg)[b]	Large carnivore	
		Lion	Spotted hyena
Buffalo	580	✔	
Bush pig	97.5		✔
Eland	570	✔	
Giraffe	900	✔	
Greater kudu	214	✔	✔
Impala	52.5		✔
Lesser kudu	81.6		✔
Warthog	82.5	✔	✔
Waterbuck	210	✔	
Zebra	400	✔	

[a] Following Hayward & Kerley (2005) and Hayward (2006).

[b] Based on Smith et al. (2003).

Table S4.2. Mean and standard deviation (in parentheses) for posterior distributions associated with environmental effects on probability of camera site occupancy for the dry seasons of 2013 and 2014, as estimated from hierarchical multi-species occupancy models. Occasion length refers to the number of days used to define detection of a species. Prey encounter rate (PER) reflects the relative usage of camera trap sites by prey species of both lions and spotted hyenas, and is defined as the number of independent camera records (> 1 hour interval) divided by the number of days the camera location was active, and multiplied by 100. Shaded cells denote significant effects.

Species	Dry season	Occasion length	Distance to water	Vegetation cover	PER
Lion	2013	1	-1.087 (1.604)	0.170 (2.573)	3.674 (2.000)
		5	-0.977 (2.023)	-0.159 (3.203)	3.680 (2.159)
		10	-1.710 (3.618)	0.409 (6.030)	4.850 (2.831)
	2014	1	-2.299 (2.413)	-5.246 (2.827)	3.512 (3.430)
		5	-2.557 (2.521)	-5.172 (3.006)	3.034 (3.519)
		10	-2.520 (2.523)	-5.287 (3.064)	3.101 (3.518)
Spotted hyena	2013	1	0.293 (0.510)	-	1.301 (0.986)
		5	0.319 (0.569)	-	1.431 (1.113)
		10	0.383 (0.700)	-	1.540 (1.210)
	2014	1	-1.386 (0.857)	-	1.368 (1.075)
		5	-1.365 (0.880)	-	1.343 (1.082)
		10	-1.312 (0.866)	-	1.401 (1.172)
Dikdik	2013	1	-1.176 (0.734)	2.410 (1.079)	-
		5	-1.190 (0.749)	2.436 (1.089)	-
		10	-1.479 (0.854)	3.005 (1.328)	-
	2014	1	-0.368 (0.507)	1.392 (0.599)	-
		5	-0.368 (0.500)	1.387 (1.059)	-
		10	-0.383 (0.525)	1.395 (0.628)	-

(Table S4.2 cont.)

Impala	2013	1	-0.007 (2.567)	0.983 (2.355)	-
		5	-0.163 (2.525)	1.061 (2.279)	-
		10	0.022 (2.527)	0.893 (2.333)	-
	2014	1	-0.415 (1.030)	-1.361 (0.981)	-
		5	-0.292 (1.159)	-1.370 (1.059)	-
		10	0.012 (1.489)	-1.007 (1.428)	-
Zebra	2013	1	-0.616 (0.535)	-0.646 (0.568)	-
		5	-0.672 (0.527)	-0.673 (0.577)	-
		10	-0.706 (0.644)	-0.693 (0.685)	-
	2014	1	-1.216 (0.854)	-2.256 (1.496)	-
		5	-1.006 (0.940)	-2.900 (2.222)	-
		10	-0.281 (1.439)	-5.265 (2.984)	-
Giraffe	2013	1	-0.141 (0.703)	0.205 (0.702)	-
		5	-0.179 (0.717)	0.211 (0.694)	-
		10	-0.142 (0.718)	0.231 (0.712)	-
	2014	1	-0.141 (3.112)	0.855 (1.890)	-
		5	-0.415 (3.191)	0.880 (1.718)	-
		10	-0.050 (3.157)	0.931 (1.782)	-

Table S4.3. Mean and standard deviation (in parentheses) for posterior distributions associated with environmental effects on probability of detection at a camera site for the dry seasons of 2013 and 2014, as estimated from hierarchical multi-species occupancy models. Occasion length refers to the number of days used to define detection of a species. Prey encounter rate (PER) reflects the relative usage of a camera trap site on a given occasion by prey species of both lions and spotted hyenas, and is defined as the number of independent camera records (> 1 hour interval) obtained during a given occasion. Shaded cells denote significant effects.

Species	Dry season	Occasion length	Distance to water	Vegetation cover	PER
Lion	2013	1	-	-	-0.111 (0.153)
		5	-	-	0.121 (0.154)
		10	-	-	0.326 (0.170)
	2014	1	-	-	0.035 (0.145)
		5	-	-	0.294 (0.123)
		10	-	-	0.359 (0.141)
Spotted hyena	2013	1	-	-	0.071 (0.061)
		5	-	-	0.043 (0.084)
		10	-	-	-0.067 (0.112)
	2014	1	-	-	0.234 (0.049)
		5	-	-	0.461 (0.087)
		10	-	-	0.499 (0.133)
Dikdik	2013	1	-0.154 (0.080)	-	-
		5	-0.034 (0.100)	-	-
		10	0.086 (0.130)	-	-
	2014	1	0.256 (0.064)	-	-

(Table S4.3 cont.)

		5	0.342 (0.104)	-	-
		10	0.508 (0.158)	-	-
Impala	2013	1	-0.740 (0.043)	-	-
		5	-0.964 (0.095)	-	-
		10	-1.150 (0.155)	-	-
	2014	1	-0.638 (0.046)	-	-
		5	-0.877 (0.110)	-	-
		10	-0.956 (0.208)	-	-
Zebra	2013	1	-0.510 (0.119)	-	-
		5	-0.387 (0.145)	-	-
		10	-0.347 (0.191)	-	-
	2014	1	-0.381 (0.119)	-	-
		5	-0.553 (0.163)	-	-
		10	-0.812 (0.209)	-	-
Giraffe	2013	1	-0.157 (0.060)	-	-
		5	-0.051 (0.083)	-	-
		10	-0.087 (0.116)	-	-
	2014	1	-0.502 (0.065)	-	-
		5	-0.430 (0.092)	-	-
		10	-0.408 (0.124)	-	-

Table S4.4. Co-detection model estimates and standard errors.

Season	Occasion length	Model	Effect	Estimate	SE
2013	1	SH	Intercept	-3.539	0.264
			Lion	1.352	0.387
			Prey	0.141	0.164
		Lion	Intercept	-5.294	0.379
			SH	1.421	0.387
			Dikdik	-0.181	1.049
			Impala	0.168	0.336
			Zebra	-0.823	1.035
			Giraffe	-0.282	0.549
	5	SH	Intercept	-2.468	0.399
			Lion	0.629	0.386
			Prey	0.861	0.329
		Lion	Intercept	-4.888	0.623
			SH	0.799	0.375
			Dikdik	-0.808	0.675
			Impala	1.322	0.574
			Zebra	-0.13	0.451
			Giraffe	0.972	0.357
	10	SH	Intercept	-1.659	0.56
			Lion	0.502	0.485
			Prey	0.706	0.502
		Lion	Intercept	-5.13	1.108
			SH	0.856	0.427
			Dikdik	-0.48	0.578
			Impala	2.014	1.067
			Zebra	-0.01	0.454
			Giraffe	0.717	0.441
2014	1	SH	Intercept	-3.33	0.23
			Lion	0.231	0.528
			Prey	0.225	0.147
		Lion	Intercept	-5.368	0.359
			SH	0.37	0.532
			Dikdik	1.268	0.5
			Impala	0.493	0.37
			Zebra	0.535	0.588
			Giraffe	-0.408	0.572
	5	SH	Intercept	-1.882	0.35
			Lion	1.05	0.398
			Prey	0.451	0.308
		Lion	Intercept	-4.095	0.488

(Table S4.4 cont.)

		SH	1.174	0.377
		Dikdik	0.094	0.522
		Impala	0.154	0.461
		Zebra	0.158	0.437
		Giraffe	0.464	0.37
10	SH	Intercept	-2.014	0.651
		Lion	0.63	0.454
		Prey	1.319	0.639
	Lion	Intercept	-3.968	0.679
		SH	0.752	0.418
		Dikdik	0.561	0.532
		Impala	0.752	0.653
		Zebra	0.056	0.46
		Giraffe	0.371	0.43

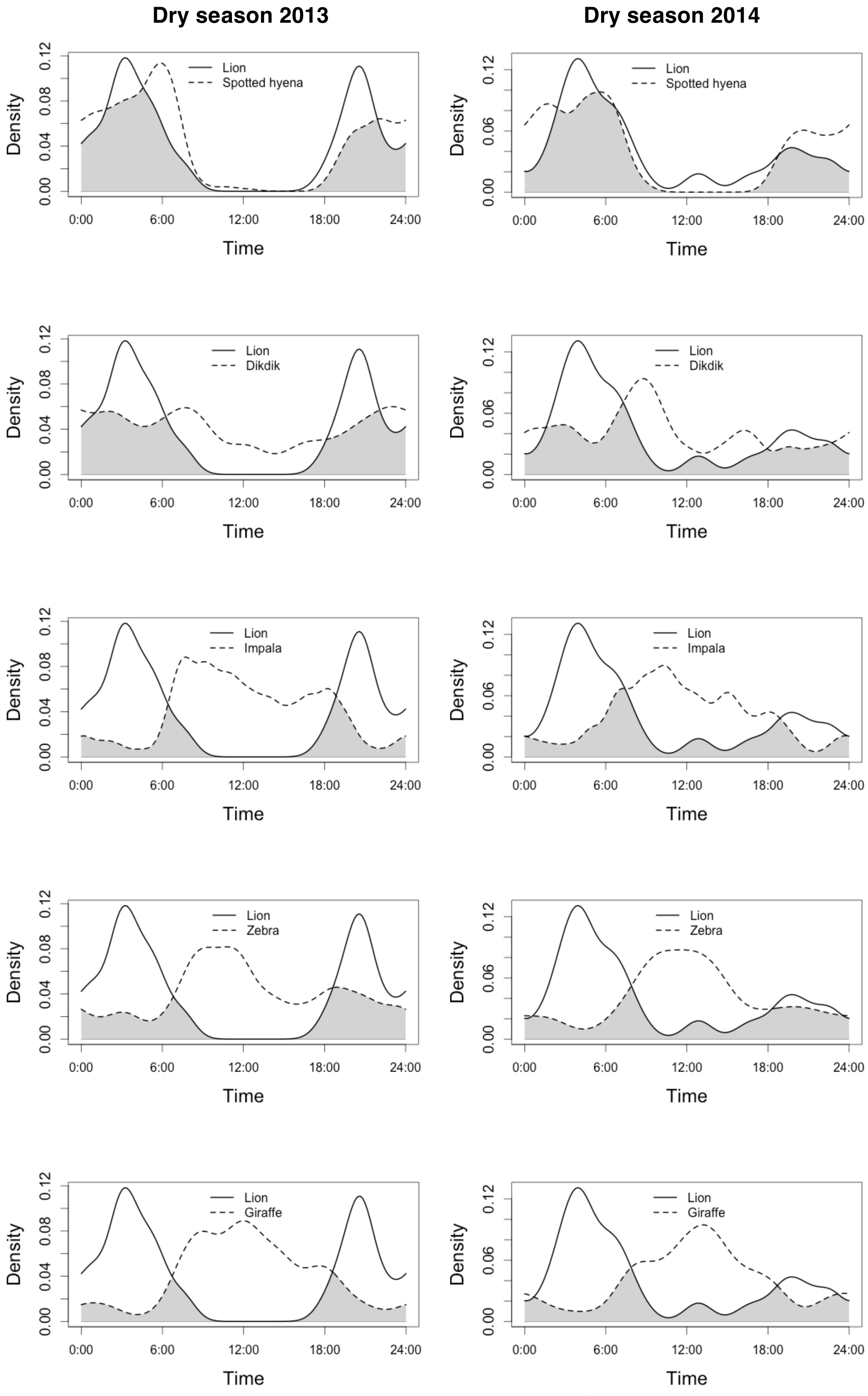

Figure S4.1. Activity pattern overlap with lions for spotted hyaena, dikdik, impala, zebra and giraffes in Ruaha during the dry seasons of 2013 and 2014. Shaded sections represent overlap between the density functions of 2 species.

REFERENCES

Abade, L., D. W. Macdonald, and A. J. Dickman (2014). Using landscape and bioclimatic features to predict the distribution of lions, leopards and spotted hyaenas in Tanzania's Ruaha landscape. *PLoS One* **9**, e96261.

Ahumada, J. A., C. E. Silva, K. Gajapersad, C. Hallam, J. Hurtado, E. Martin, A. McWilliam, B. Mugerwa, T. O'Brien, F. Rovero, D. Sheil, W. R. Spironello, N. Winarni, and J. A. Andelman (2011). Community structure and diversity of tropical forest mammals: data from a global camera trap network. *Philosophical Transactions of the Royal Society B: Biological Sciences* **366**, 2703–2711.

Alexander, J. S., J. J. Cusack, C. Pengju, S. Kun, and P. Riordan (2015). Conservation of snow leopards: spill-over benefits for other carnivores? *Oryx*, DOI: 10.1017/S0030605315001040.

Bischof, R., H. Ali, M. Kabir, S. Hameed, and M. A. Nawaz (2014). Being the underdog: an elusive small carnivore uses space with prey and time without enemies. *Journal of Zoology* **293**, 40–48.

Bolker, B. M., M. E. Brooks, C. J. Clark, S. W. Geange, J. R. Poulsen, M. H. H. Stevens, and J. S. S. White (2009). Generalized linear mixed models: a practical guide for ecology and evolution. *Trends in Ecology and Evolution* **24**, 127–135.

Brockmann, H. J., and C. J. Barnard (1979). Kleptoparasitism in birds. *Animal Behaviour* **27**, 487–514.

Broekhuis, F., G. Cozzi, M. Valeix, J. W. McNutt, and D. W. Macdonald (2013).

Risk avoidance in sympatric large carnivores: reactive or predictive? *Journal of Animal Ecology* **82**, 1098–1105.

Burton, A. C., E. Neilson, D. Moreira, A. Ladle, R. Steenweg, J. T. Fisher, E. Bayne, and S. Boutin (2015). Wildlife camera trapping: a review and recommendations for linking surveys to ecological processes. *Journal of Applied Ecology* **52**, 675–685.

Carbone, C., S. Christie, K. Conforti, T. Coulson, N. Franklin, J. R. Ginsberg, M. Griffiths, J. Holden, K. Kawanishi, M. Kinnaird, R. Laidlaw, A. Lynam, D. W. Macdonald, D. Martyr, C. MacDougal, L. Nath, T. O'Brien, J. Seidensticker, D. J. L. Smith, M. Sunquist, R. Tilson, and W. N. Shahruddin (2001). The use of photographic rates to estimate densities of tigers and other cryptic mammals. *Animal Conservation* **4**, 75–79.

Cooper, S. M., K. E. Holekamp, and L. Smale (1999). A seasonal feast: long-term analysis of feeding behaviour in the spotted hyaena (*Crocuta crocuta*). *African Journal of Ecology* **37**, 149–160.

Cooper, S. (2008). Optimal hunting group size: the need for lions to defend their kills against loss to spotted hyaenas. *African Journal of Ecology* **29**, 130–136.

Courbin, N., D. Fortin, C. Dussault, V. Fargeot, and R. Courtois (2013). Multi-trophic resource selection function enlightens the behavioural game between wolves and their prey. *Journal of Animal Ecology* **82**, 1062–1071.

Courbin, N., A. J. Loveridge, D. W. Macdonald, H. Fritz, M. Valeix, E. T.

Makuwe, and S. Chamaillé-Jammes (2015). Reactive responses of zebras to lion encounters shape their predator–prey space game at large scale. *Oikos*, DOI: 10.1111/oik.02555.

Cusack, J. J., A. J. Dickman, J. M. Rowcliffe, C. Carbone, D. W. Macdonald, and T. Coulson (2015). Random versus game trail-based camera trap placement strategy for monitoring terrestrial mammal communities. *PLoS One* **10**, e0126373.

Cusack, J. J., A. J. Dickman, J. M. Rowcliffe, C. Carbone, D. W. Macdonald, and T. Coulson (2015b). Data from: Random versus game trail-based camera trap placement strategy for monitoring terrestrial mammal communities. Dryad Digital Repository: http://datadryad.org/resource/ doi:10.5061/dryad.br86d

Efford, M. G. and D. K. Dawson (2012). Occupancy in continuous habitat. *Ecosphere*, DOI: http://dx.doi.org/10.1890/ES11-00308.1.

Foster, V. C., P. Sarmento, R. Sollmann, N. Tôrres, A. T. Jácomo, N. Negrões, C. Fonseca, and L. Silveira (2013). Jaguar and puma activity patterns and predator-prey interactions in four Brazilian biomes. *Biotropica* **45**, 373–379.

Gelman, A., and D. B. Rubin (1992). Inference from iterative simulation using multiple sequences. *Statistical Science* **7**, 457–472.

Guillera-Arroita, G., M. S. Ridout, B. J. Morgan (2010). Design of occupancy studies with imperfect detection. *Methods in Ecology and Evolution* **1**, 131–139.

Guillera-Arroita, G., B. J. Morgan, M. S. Ridout, and M. Linkie (2011). Species occupancy modeling for detection data collected along a transect. *Journal of Agricultural, Biological, and Environmental Statistics* **16**, 301–317.

Hayward, M. W. (2006). Prey preferences of the spotted hyaena (*Crocuta crocuta*) and degree of dietary overlap with the lion (*Panthera leo*). *Journal of Zoology* **270**, 606–614.

Hayward, M. W. and G. I. Kerley (2005). Prey preferences of the lion (*Panthera leo*). *Journal of Zoology* **267**, 309–322.

Hayward, M. W. and G. J. Hayward (2007). Activity patterns of reintroduced lion *Panthera leo* and spotted hyaena *Crocuta crocuta* in the Addo Elephant National Park, South Africa. *African Journal of Ecology* **45**, 135–141.

Hayward, M. W., and R. Slotow (2009). Temporal partitioning of activity in large African carnivores: tests of multiple hypotheses. *South African Journal of Wildlife Research* **39**, 109–125.

Hopcraft, J. G. C., A. R. E. Sinclair, and C. Packer (2005). Planning for success: Serengeti lions seek prey accessibility rather than abundance. *Journal of Animal Ecology* **74**, 559–566.

Höner, O. P., B. Wachter, M. L. East, and H. Hofer (2002). The response of spotted hyaenas to long-term changes in prey populations: functional response and interspecific kleptoparasitism. *Journal of Animal Ecology* **71**, 236–246.

Kays, R., R. Costello, T. Forrester, M. C. Baker, A. W. Parsons, E. L. Kalies, G. Hess, J. J. Millspaugh, and W. McShea (2015). Cats are rare where coyotes roam. *Journal of Mammalogy* **96**, 981–987.

Kruuk, H. (1972). *The spotted hyaena: a study of predation and social behavior.* University of Chicago Press, Chicago.

Latombe, G., D. Fortin, and L. Parrott (2014). Spatio-temporal dynamics in the response of woodland caribou and moose to the passage of grey wolf. *Journal of Animal Ecology* **83**, 185–198.

Laundré, J. W., L. Hernández, and K. B. Altendorf (2001). Wolves, elk, and bison: reestablishing the" landscape of fear" in Yellowstone National Park, USA. *Canadian Journal of Zoology* **79**, 1401–1409.

Lesmeister, D. B., C. K. Nielsen, E. M. Schauber, and E. C. Hellgren (2015). Spatial and temporal structure of a mesocarnivore guild in midwestern north America. *Wildlife Monographs* **191**, 1–61.

Linkie, M., Y. Dinata, A. Nugroho, and I. A. Haidir (2007). Estimating occupancy of a data deficient mammalian species living in tropical rainforests: sun bears in the Kerinci Seblat region, Sumatra. *Biological Conservation* **137**, 20–27.

Linkie, M., and M. S. Ridout (2011). Assessing tiger–prey interactions in Sumatran rainforests. *Journal of Zoology* **284**, 224–229.

Long, J. A., T. A. Nelson, S. L. Webb, and K. L. Gee (2014). A critical examination of indices of dynamic interaction for wildlife telemetry studies. *Journal of Animal Ecology* **83**, 1216–1233.

MacKenzie, D. I., J. D. Nichols, G. B. Lachman, S. Droege, J. A. Royle, and C. A. Langtimm (2002). Estimating site occupancy rates when detection probabilities are less than one. *Ecology* **83**, 2248–2255.

MacKenzie, D. I., L. L. Bailey, and J. Nichols (2004). Investigating species co-occurrence patterns when species are detected imperfectly. *Journal of Animal Ecology* **73**, 546–555.

MacKenzie, D. I. (2006). Modeling the probability of resource use: the effect of, and dealing with, detecting a species imperfectly. *The Journal of Wildlife Management* **70**, 367–374.

Meredith, M., and M. S. Ridout (2014). overlap: estimates of coefficients of overlapping for animal activity patterns. 0.2.2. edn, project.org/package=overlap

Miller, D. A., L. L. Bailey, E. H. C. Grant, B. T. McClintock, L. A. Weir, and T. R. Simons (2015). Performance of species occurrence estimators when basic assumptions are not met: a test using field data where true occupancy status is known. *Methods in Ecology and Evolution* **6**, 557–565.

Muneza, A. B., R. A. Montgomery, J. T. Fennessy, A. J. Dickman, G. J. Roloff, and D. W. Macdonald (2016). Regional variation of the manifestation, prevalence, and severity of giraffe skin disease: a review of an emerging disease in wild and captive giraffe populations. *Biological Conservation* **198**, 145–156.

O'Connell, A. F., J. D. Nichols, and K. U. Karanth (2010). *Camera traps in animal ecology: methods and analyses*. Springer, Tokyo.

Périquet, S., H. Fritz, and E. Revilla (2015). The Lion King and the Hyaena Queen: large carnivore interactions and coexistence. *Biological Reviews* **90**, 1197–1214.

Plummer, M. (2014). rjags: Bayesian graphical models using MCMC. R package version 3-14. http://CRAN.R-project.org/package=rjags

Potts, J. R., K. Mokross, and M. A. Lewis (2014). A unifying framework for quantifying the nature of animal interactions. *Journal of The Royal Society Interface* **11**, 20140333.

R Development Core Team (2014). R: a language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. www.rproject.org

Ridout, M. S., and M. Linkie (2009). Estimating overlap of daily activity patterns from camera trap data. *Journal of Agricultural, Biological, and Environmental Statistics* **14**, 322–337.

Robinson, Q. H., D. Bustos, and G. W. Roemer (2014). The application of occupancy modeling to evaluate intraguild predation in a model carnivore system. *Ecology* **95**, 3112–3123.

Ross, J., A. J. Hearn, P. J. Johnson, and D. W. Macdonald (2013). Activity patterns and temporal avoidance by prey in response to Sunda clouded leopard predation risk. *Journal of Zoology* **290**, 96–106.

Rovero, F., F. Zimmermann, D. Berzi, and P. Meek (2013). " Which camera trap type and how many do I need?" A review of camera features and study designs for a range of wildlife research applications. *Hystrix, the*

Italian Journal of Mammalogy **24**, 148–156.

Rowcliffe, J. M., R. Kays, B. Kranstauber, C. Carbone, and P. A. Jansen (2014). Quantifying levels of animal activity using camera trap data. *Methods in Ecology and Evolution* **5**, 1170–1179.

Schaller, G. B. (1972). *The Serengeti lion: a study of predator-prey relations.* University of Chicago Press, Chicago.

Schuette, P., A. P. Wagner, M. E. Wagner, and S. Creel (2013). Occupancy patterns and niche partitioning within a diverse carnivore community exposed to anthropogenic pressures. *Biological Conservation* **158**, 301–312.

Sih, A. (1984). The behavioural response race between predator and prey. *The American Naturalist* **123**, 143–150.

Smith, F. A., S. K. Lyons, S. M. Ernest, K. E. Jones, D. M. Kaufman, T. Dayan, P. A. Marquet, J. H. Brown, and J. P. Haskell (2003). Body mass of late quaternary mammals: Ecological Archives E084-094. *Ecology* **84**, 3403–3403.

Sollmann, R., M. M. Furtado, H. Hofer, A. T. Jácomo, N. M. Tôrres, and L. Silveira (2012). Using occupancy models to investigate space partitioning between two sympatric large predators, the jaguar and puma in central Brazil. *Mammalian Biology-Zeitschrift für Säugetierkunde* **77**, 41–46.

Stolberger, S. (2012). *Ruaha National Park: an intimate view.* Sue Stolberger, Tanzania.

Su, Y. S., and M. Yajima (2012). R2jags: a package for running jags from R. R package version 0.03-08, URL http://CRAN. R-project. org/package= R2jags.

Sunarto, S., M. J. Kelly, K. Parakkasi, and M. B. Hutajulu (2015). Cat coexistence in central Sumatra: ecological characteristics, spatial and temporal overlap, and implications for management. *Journal of Zoology* **296**, 104–115.

Suselbeek, L., W. Emsens, B. T. Hirsch, R. Kays, J. M. Rowcliffe, V. Zamora-Gutierrez, and P. A. Jansen (2014). Food acquisition and predator avoidance in a Neotropical rodent. *Animal Behaviour* **88**, 41–48.

Swanson, A., T. Caro, H. Davies-Mostert, M. G. Mills, D. W. Macdonald, M. Borner, E. Masenga, and C. Packer (2014). Cheetahs and wild dogs show contrasting patterns of suppression by lions. *Journal of Animal Ecology* **83**, 1418–1427.

Tambling, C. J., L. Minnie, J. Meyer, E. W. Freeman, R. M. Santymire, J. Adendorff, and G. I. Kerley (2015). Temporal shifts in activity of prey following large predator reintroductions. *Behavioral Ecology and Sociobiology* **69**, 1153–1161.

Thorn, M., D. M. Scott, M. Green, P. W. Bateman, and E. Z. Cameron (2009). Estimating brown hyaena occupancy using baited camera traps. *South African Journal of Wildlife Research* **39**, 1–10.

Tilman, D., and P. M. Kareiva (1997). *Spatial ecology: the role of space in population dynamics and interspecific interactions*. Princeton University

Press, Princeton.

Trinkel, M. and G. Kastberger (2005). Competitive interactions between spotted hyenas and lions in the Etosha National Park, Namibia. *African Journal of Ecology* **43**, 220–224.

Vanak, A. T., D. Fortin, M. Thaker, M. Ogden, C. Owen, S. Greatwood, and R. Slotow (2013). Moving to stay in place: behavioral mechanisms for coexistence of African large carnivores. *Ecology* **94**, 2619–2631.

Waddle, J. H., R. M. Dorazio, S. C. Walls, K. G. Rice, J. Beauchamp, M. J. Schuman, and F. J. Mazzotti (2010). A new parameterization for estimating co-occurrence of interacting species. *Ecological Applications* **20**, 1467–1475.

Watts, H. E. and K. E. Holekamp (2008). Interspecific competition influences reproduction in spotted hyenas. *Journal of Zoology* **276**, 402–410.

Chapter 5

Characterising the spatial response of elk to wolves in Yellowstone's Northern Range: a null model approach

- Running head -

Spatial response of elk to wolves

- Title -

Characterising the spatial response of elk to wolves in Yellowstone's Northern Range: a null model approach

- Authors -

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ABSTRACT

Overlap in long-term space use and encounter rates represent two useful metrics for quantifying the proactive (i.e. long-term) and reactive (i.e. short-term) responses of prey to predator movements from telemetry data. Interpreting such measures is often hindered by lack of an appropriate null model of random movement with which to generate expected values, as well as uncertainties arising from inconsistent or low fix frequencies, which may lead to an under-estimation of the frequency of encounter between individuals. Here, we assess how these two sources of bias can affect the characterisation of elk (*Cervus elaphus*) responses to the distribution and movement of grey wolves (*Canis lupus*) in northern Yellowstone National Park during the winter of 2013-14. We compare the response outcomes of 18 elk obtained from three different null model formulations (rotation, rotation and shift, and correlated random walk) and two different types of wolf trajectories, the latter differing in the consistency of the frequency used to record locations (1 hour versus a mixture of 1 hour and 6 hour periods). Overall, we reveal an absence of significant avoidance behaviour for the majority of elk considered. Those individuals that did show a significantly lower spatial overlap (4 out of 18 elk) than expected were not consistent across null models, highlighting the potential sensitivity of the approach to model formulation. Although standardising wolf fix frequency to 1 hour led to an increase in the total number of encounters recorded, from 66 to 117, it had a negligible effect on whether elk were perceived to actively minimise instances of close proximity, instead leading to a stronger positive linear

relationship between spatial overlap and encounter rate. Our study suggests that predator-prey interactions may not always result in measurable spatial responses of prey to predator movement.

INTRODUCTION

Global Positioning Satellite (GPS) telemetry is increasingly being used to quantify spatial relationships between the movement patterns of different individuals and species, often with a view to inferring on intra- and inter-specific interactions, respectively (Kays et al. 2015). In particular, measures of spatial overlap and encounter rate, which respectively quantify the level of joint space use exhibited by two individuals (Kernohan et al. 2001, Millspaugh et al. 2004, Fieberg & Kochanny 2005) and the degree to which their trajectories “meet” one another over time (Macdonald et al. 1980, Doncaster 1990), have provided useful and intuitive indices of the potential for interaction (Benhamou et al. 2014, Long et al. 2014). Such measures have primarily been used to gain insights into competitive and social interactions between individuals of the same species (Walrath et al. 2011, Robert et al. 2012, Lührs and Kappeler 2013, Miller 2015), as well as the potential for disease transmission across species (Proffitt et al. 2010, Barasona et al. 2014, Williams et al. 2014). However, measures of spatial overlap and encounter rate have rarely been considered simultaneously when attempting to characterise avoidance behaviour in the context of predator-prey interactions (Valeix et al. 2009).

The spatial response of prey to the movement of predators is an important component of predator-prey interactions (Sih 1984, 1998), providing valuable insights into the role of non-consumptive effects of predators in structuring mammal communities (Weissberg et al. 2014). Predator avoidance can occur over large spatial scales (i.e. several kilometres), with prey proactively avoiding areas that are preferentially used by predators (Thaker et al. 2011). This approach usually assumes that the spatial distribution of a predator reflects a heterogeneous landscape of long-term predation risk (Lima & Dill 1990, Thaker et al. 2011, Kauffman et al. 2007, Searle et al. 2008). Under this scenario, prey can be expected to avoid areas of high risk (i.e. peaks in the predator's distribution) and focus their spatial activity in so-called refugia (i.e. troughs) (Laundré et al. 2001, Laundré 2010), thereby reducing spatial overlap. In addition, prey may exhibit reactive movement responses, defined as sudden displacements following detection of a predator in the immediate surroundings (Creel et al. 2008, Courbin et al. 2013, Middleton et al. 2013, Basille et al. 2015). Although the distance over which prey initiate reactive responses can vary depending on age, group size, body condition, and the type of habitat available nearby (Liley & Creel 2008, Basille et al. 2015, Courbin et al. 2015), in general it can be expected that instances of close proximity (i.e. potential encounters) will be observed less often if prey respond reactively to predators than if they move randomly with reference to them.

Although measures of spatial overlap and encounter rate have the potential to advance our understanding of the spatial responses of prey to predators, their interpretation is often hindered by lack of an appropriate null model of random movement with which to generate expected values (Gotelli & Graves 1996, Richard et al. 2013, Miller 2015). Typically, a null model generates a pattern based on randomisation that lacks some process or mechanisms of interest to test its influence (Gotelli & Graves 1996). This approach has been used extensively in community ecology to investigate niche overlap and species co-occurrence through the simulation of "pseudo-communities" in which underlying processes, such as competition, are supposedly absent (Pianka 1986, Gotelli & Graves 1996, Gotelli 2000, O'Sullivan & Perry 2013). Recently, Richard et al. (2013) extended the application of null models to examine the potential for spatial interactions between female red and roe deer (*Cervus elaphus* and *Capreolus capreolus*, respectively). They did this by randomly permuting and shifting roe deer trajectories to obtain "pseudo-trajectories", re-calculating the level of overlap with the distribution of female red deer to generate an expected distribution. The authors find that spatial interaction outcomes between the two species varied depending on the null model formulation used to generate "pseudo-trajectories", that is, the nature of the constraints imposed on the simulation procedure. Furthermore, they did not apply their null model approach to assess whether trajectories of the two species encountered each other less than expected by chance.

In this study, we assess how null model choice can affect the characterisation of elk (*Cervus elaphus*) spatial responses to the distribution and movement of grey wolves (*Canis lupus*) in the Northern Range (NR) of Yellowstone National Park (YNP). We quantify spatial overlap and encounter rates between GPS-collared elk and wolves during the winter of 2013-14, and determine whether these are significantly lower than expected if the long- and short-term movements of elk were random with reference to those of wolves, respectively. To carry out this latter step, we implement three different null model formulations that generate alternative elk trajectories within the same geographic locality as the observed, thus accounting for the species' philopatric behaviour (Brough 2009, Gower et al. 2008). We hypothesise that, if elk respond proactively to the distribution of wolves, they should show lower than expected spatial overlap. If, on the other hand, elk response is reactive, they should actively minimise encounter rates with wolves. We test whether elk show either or both of these types of responses.

METHODS

Study area

Northern Yellowstone National Park encompasses roughly 1,000 km^2 of mountainous terrain and open valleys, with elevation ranging from 1,500 to 3,210 m (Houston 1982). The area defines the northern ungulate winter range, and is largely composed of shrub steppe, with patches of intermixed lodgepole pine (*Pinus contorta*), Douglas fir (*Pseudotsuga menziesii*), Engelmann spruce (*Picea engelmanni*), and aspen stands (Houston 1982, Despain 1990). Winters in the study area are usually cold and snowy.

Annual elk counts in the NR averaged 4,499 individuals between the years 2010 and 2015 (range: 3,915 – 4,912), although no count was performed in 2013. Smith et al. (2014) reported five wolf packs/groups as active in the

NR over the year 2013, although two of these – 8 Mile and Junction Butte packs – were considerably larger than the others, accounting for 27 individuals out of a total of 34 recorded. In early 2014, the largest packs in the NR included 8 Mile, Junction Butte and the newly formed Prospect Peak (Smith et al. 2015). Elk were the dominant prey of NR wolves in both 2013 and 2014 (Smith et al. 2014, 2015).

GPS-collar data

We considered GPS collar data collected on 4 wolves (n=4 packs) and 18 elk between 1st November 2013 and 30th April 2014 (Figure 5.1a). Wolf collars (Lotek Iridium Collars, Newmarket, Ontario, Canada) were programmed to record one relocation every hour between 14th November and 15th December 2013, and between 28th February and 31st March 2014. During these periods, trajectories were used by the Yellowstone Wolf Project (YWP) to identify potential kill sites (M. Metz, pers. coms.). Outside of these periods, wolf collars recorded at a frequency of one relocation every six hours, which enabled the YWP to relocate wolf packs for routine monitoring. In both cases, recorded data were uploaded via Iridium satellite every 12 fixes, and available to download from a dedicated webserver. Hereafter, wolf trajectories including both 1-hour and 6-hour fix frequencies are referred to as original trajectories (see below for details on how these were standardised). We assumed that the recorded movement trajectories reflected those of corresponding packs (Benson & Patterson 2015). To avoid duplicated trajectories derived from wolves belonging to the same pack, which could bias subsequent estimation of wolf space use (see below), we plotted a time series of the distances between simultaneous relocations obtained for each wolf dyad. Based on this, we excluded one set of relocations during periods of joint movement (if any).

In contrast, elk collars (also Lotek Iridium Collars) were programmed to record one relocation on average every 2.5 hours throughout the period considered. Data upload and download options were similar to those used for wolf collars. To verify the assumption that each elk moved independently from the others, we calculated an index of movement cohesion for every elk dyad (n = 306). We used Shirabe's (2006) correlation coefficient, which measures the degree of correlation between the movement paths of two individuals as a multivariate Pearson product-moment correlation coefficient (Shirabe 2006, Long et al. 2014). The index ranges from -1 (negative correlation) to 1 (positive correlation), with 0 indicating random movement, but does not consider the relative distance between simultaneous relocations. Similarly to wolf dyads, we also measured the average distance between simultaneous relocations.

Spatial overlap

We defined spatial overlap as the level of similarity between the utilisation distribution (UD) of a single elk and a joint wolf UD representing the combined spatial activity of all collared wolves (Figure 5.1b and c). The latter was taken as the product of individual wolf UDs – each of these weighted by the size of the corresponding pack (YNP unpublished data, Kauffman et al.

2007) – and scaled to sum to unity. For both species, UDs were estimated over a continuous grid of cell size 1 by 1 km using a Brownian bridge movement model (BBMM) implemented in the R package BBMM (Bullard 1999, Horne et al. 2007). The BBMM is a continuous-time stochastic movement model, where the probability of being in an area is conditioned on 1) the distance and elapsed time between successive locations, 2) a measure of location error (here set to 50 m), and 3) an estimate of the animal's mobility (the Brownian motion variance, see Horne et al. 2007). Strictly speaking, the model approximates the movement path between two subsequent locations by applying a conditional random walk. This approach has been adopted as a superior alternative to more traditional fixed kernel density estimation methods (Calenge 2006), which apply a constant smoothing parameter across relocations. Because UD tails (i.e. beyond the 95 % isopleth) tend to be poorly estimated, we generated conditional 95 % UDs scaled to sum to unity (Benhamou et al. 2014).

Spatial overlap was measured as Bhattacharyya's coefficient (BA), a product-based similarity index used to describe the level of affinity between two overlapping distributions (Bhattacharyya 1943, Fieberg & Kochanny 2005). The BA index, which ranges from 0 (no overlap) to 1 (complete overlap), has been widely used to compare UDs in a range of different taxa (Fieberg & Kochanny 2005). If UD_A and UD_B are the estimated utilisation distributions for individuals A and B, respectively, then

$$BA = \iint_{-\infty -\infty}^{\infty \infty} \sqrt{UD_A(x,y)} \times \sqrt{UD_B(x,y)}\, dxdy$$

We calculated the BA coefficient based on conditional 95 % UDs, so as to minimise bias associated with the poorly estimated UD tails (Fieberg 2007, Benhamou et al. 2014). Given the substantial difference in the average home range size of wolves and elk (see Figure 5.1b for an example), we expected BA values to be closer to 0 than to 1. However, we stress that this in itself cannot be considered as evidence for proactive avoidance behaviour, and is the reason why we implemented a null model approach (see below).

Encounter rate

We measured the rate at which a given elk encountered wolves as ER = ST/n where n represents the total number of fixes recorded for a given elk, and ST is the total number of recorded encounters with wolves. Encounters consisted of spatially proximal and temporally simultaneous elk and wolf fixes defined according to specific distance d and time t thresholds, respectively (following Long et al. 2014). We set d to 1000 m following Middleton et al. (2013), who found that elk tended to increase their rates of movement, displacement and vigilance when wolves were within this distance threshold. Temporal proximity t was set to 1 hour as this represented the maximum length of a wolf hunt (MacNulty 2002). Thus, if elk and wolf relocations obtained in the same 1-hour window were observed to be within 1000 m of one another, they constituted an encounter. Importantly, we use the term “encounter” to denote a significantly increased likelihood for a potentially lethal interactive event (i.e. a hunt) to occur, which we assume would be actively avoided by elk (Creel et al. 2005, Proffitt et al. 2009, Latombe et al. 2014).

Standardising wolf fix frequency

The wolf relocation data used in this study was characterised by periods of high (~ 1 hour) and low (~ 6 hours) fix frequency. We hypothesised that proximal movements between elk and wolves might go undetected during periods of low fix frequency, thereby biasing estimation of encounter rates (Creel et al. 2013). Consequently, we tested whether standardising the relocation rate of wolves to 1 fix every hour throughout the period of study would influence measures of ER, and by extension, whether or not elk would be perceived to encounter wolves less than expected by chance. We did this by simulating additional points between consecutive wolf relocations separated by six hours prior to estimating the ER index. Simulated paths, which we refer to as standardised wolf trajectories, were also based on a Brownian bridge movement model formulation and implemented using the R function *simm.bb* in package adehabitatLT (Calenge 2006).

Null model

We used a null model approach to determine whether the observed spatial overlap and encounter rate were less than expected if a given elk moved randomly with reference to wolves. We implemented three different null model formulations to generate alternative elk trajectories within the NR boundary. The first randomly rotated the observed elk trajectory around its centre of gravity (Rotation model, Figure 5.1d), thus maintaining its inherent structure. The second formulation randomly rotated the trajectory, but in addition shifted its centre of gravity to a randomly sampled relocation in the original trajectory (RSH model, Figure 5.1e). Finally, the third formulation randomly sampled the distributions of step lengths and turning angles derived from the observed trajectory to construct a correlated random walk (CRW model, Figure 5.1f) from the original starting location. Thus, all formulations maintained alternative elk trajectories within the same geographical area as the original, thereby reflecting the species' philopatric behaviour (average annual home range shift in YNP: median = 109.90 meters, n = 128; M. Kohl, unpublished data), which we hypothesised would limit their ability to modulate spatial activity over the entire NR area. Since individual elk UDs generally covered a much smaller area than the joint wolf UD, and were typically contained within the latter, our null model approach specifically tests whether elk are able to exploit "troughs" in wolf spatial activity within a given geographic locality, thus minimising overall spatial overlap (Figure 5.1c).

For each elk and null model formulation, we generated 1,000 null trajectories, each time re-calculating the BA index with the original wolf trajectories, and the ER index with both the original and standardised wolf trajectories. Randomisations were carried out using the *NMs.randomCRW* and *NMs.randomShiftRotation* functions in the R package adehabitatLT (Calenge 2006). Statistical testing consisted in computing the one-tailed probability $P = (k_e + 1)/k$ of getting a value equal to or less than the observed level, where k is the total number of null elk trajectories and k_e is the number of values < observed. All analyses were carried out in R version 3.2.1 (R Development Core Team 2015) and all statistical tests were based on an alpha level of 0.05.

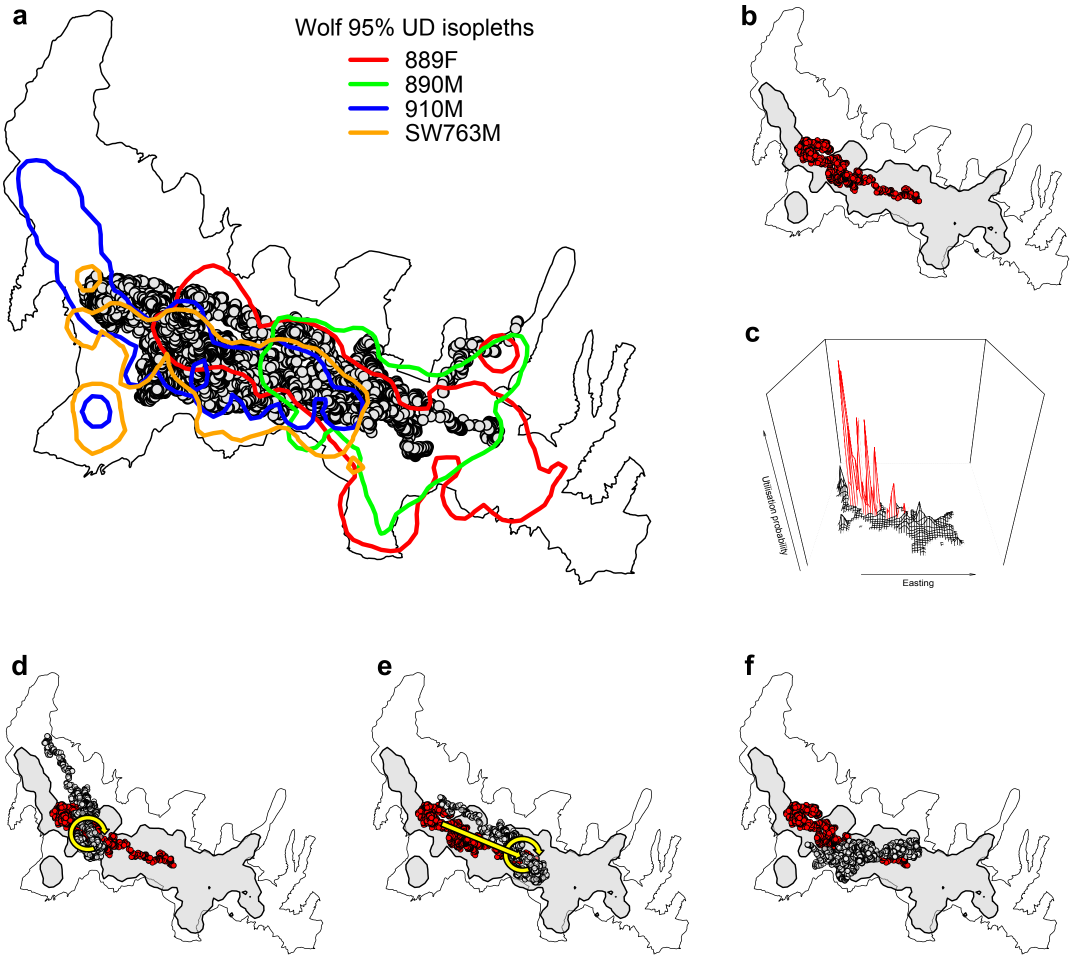

Figure 5.1. (**a**) Distribution of elk GPS-collar relocations (grey dots) relative to the 95 % contour isopleths of four wolves (see legend) in Yellowstone's Northern Range during the winter of 2013-14. (**b**) Example illustrating the size of the elk trajectory covering the most area (red dots) relative to the 95 % contour isopleth of the joint wolf UD (grey polygon). (**c**) 3-dimensional representation of an example elk UD (red) overlapping with the joint wolf (black), both scaled to sum to unity. Spatial overlap was estimated as Battacharyya's affinity coefficient between the two UDs. The bottom row illustrates an example elk trajectory obtained from each of the different null model formulations: (**d**) Rotation model, (**e**) RSH model, and (**f**) CRW model. In (**d**) and (**e**), yellow arrows clarify the rotation and shifting steps.

RESULTS

Between 1st November 2013 and 30th April 2014, we collected 7,168 and 28,437 relocations from 4 wolf and 18 elk collars, respectively. Elk trajectories averaged 1,580 relocations (SD = 190.5) and 167 days of tracking (SD = 19.8) over the study period. Elk movements tended to show low cohesion, with an average correlation coefficient across elk dyads of 0.06 (Figure S5.1a). In addition, the average distance between simultaneous relocations within an elk pair showed two peaks at around 5 and 20 km, with the overall mean of the resulting distribution being 12.4 km (Figure S5.1b). Together, these measures support the assumption that the elk trajectories were independent, and consequently no elk trajectories were excluded from our analysis.

Details pertaining to each wolf trajectory, including the number of relocations added to standardise fix frequency to 1 hour, are summarised in Table 5.1. Two of the wolves considered, SW763M and 910M, exhibited joint movement as part of the 8 Mile pack between 13th December 2013 (when 910M was collared) and 21st January 2014, following which period SW763M dispersed to form the Prospect Peak pack (Smith et al. 2015, Figure S5.2). We therefore only considered relocations of 910M collected after 21st January 2014. This enabled us to assume that each collared wolf belonged to one of the dominant packs known to use the NR during the winter of 2013-14 (Table 5.1).

The estimated 95 % contour isopleth of the joint wolf UD covered a much larger area than that of individual elk (747.7 km^2 versus a mean of 58.3 [range 7.3 – 162.1] for elk), and consequently, observed spatial overlap was generally low, ranging from 0.05 to 0.26. Encounter events, defined as wolf and elk relocations obtained during the same 1-hour window and observed to be within 1000 m of one another, occurred regularly throughout the period of study (Figure 5.2). Standardisation of wolf fix frequency to 1 hour led to an increase in the total number of encounters recorded, from 66 to 117. This was coupled with a significant increase in encounter rates measured at the level of individual elk (paired Wilcoxon signed rank: V = 102, $P < 0.01$; Figure 5.2).

The majority of elk considered (14 out of 18) did not show a tendency to proactively avoid areas that were highly used by collared wolves, regardless of the null model formulation used to generate alternative trajectories (Table 5.2). Most notably, the RSH Model did not allow the null hypothesis of random or higher spatial overlap to be rejected for any of the elk considered, while the Rotation and CRW formulations produced contradictory outcomes for three individuals out of the four showing potential for spatial avoidance (elks 32313, 35029 and 35032; Table 5.2). It is important to note that individual elk showing the lowest observed spatial overlap with wolves were the ones most likely to result in a significant outcome. Lastly, null model formulations differed in the mean and variance of the resulting expected distributions for spatial overlap (Figure 5.3a, Figure S5.3). In particular, expected distributions from the RSH and CRW formulations showed higher variances than those from the Rotation model (Wilcoxon rank sum test: $W_{Rotation\text{-}RSH} = 25$ and $W_{Rotation\text{-}CRW} = 9$, both $P < 0.001$), although the latter produced a mean expected value for spatial overlap that was very similar to the observed.

No elk was found to exhibit a significantly lower than expected encounter rate with original wolf trajectories (Table 5.3, Figures S5.4 and S5.5). Standardising wolf fix frequency to 1 hour had little effect on this outcome, with only one elk showing potential for reactive avoidance behaviour, albeit very marginally (P = 0.046). In addition, we found a positive relationship between spatial overlap and encounter rate, which was found to be stronger when estimation of the latter metric was based on standardised wolf trajectories (R^2 = 0.42, df = 16, P < 0.01 versus R^2 = 0.11, df = 16, P = 0.074 when original wolf trajectories were used; Figure 5.4).

Table 5.1. Details relating to GPS-collared wolves. Original wolf trajectories combined periods of low (~6 hours) and high (~1 hour) fix frequency, whilst standardised trajectories were characterised by a constant 1-hour fix frequency.

Wolf ID	Pack	Pack size (adults)	# days tracked	# original relocations	# standardised relocations
889F	755M/889F Group	2	181	1891	4326
890M	Junction Butte	5	181	2027	4363
910M	8 Mile	9	139	1268	3334
SW763M	Prospect Peak	3	181	1982	4330

Table 5.2. Observed and expected spatial overlap with wolves for 18 GPS-collared elk. The expected value represents the mean of a null distribution generated by randomly rotating the observed elk trajectory around its centre of gravity (Rotation Model), randomly rotating and shifting the centre of gravity to a randomly selected relocation in the observed trajectory (RSH Model), and randomly sampling the distributions of step lengths and turning angles derived from the observed trajectory to construct a new correlated random walk (CRW Model). Shaded cells indicate elk showing a level of spatial overlap with wolves that was lower than expected (one-tailed test, α = 0.05).

Elk ID		Rotation Model		RSH Model		CRW Model	
	Observed	Expected	*P*	Expected	*P*	Expected	*P*
32298	0.244	0.229	0.812	0.184	0.871	0.26	0.347
32299	0.248	0.227	0.842	0.211	0.881	0.245	0.545
32300	0.235	0.197	0.852	0.22	0.535	0.31	0.109
32302	0.103	0.105	0.376	0.117	0.267	0.051	0.851
32312	0.181	0.171	0.772	0.093	0.990	0.198	0.327
32313	0.098	0.125	0.267	0.097	0.456	0.202	< 0.05
32315	0.215	0.213	0.574	0.21	0.535	0.239	0.218
32408	0.194	0.177	0.921	0.117	0.980	0.175	0.673
33609	0.047	0.065	< 0.05	0.07	0.158	0.123	< 0.01
33610	0.263	0.198	0.960	0.184	0.792	0.313	0.178
33611	0.196	0.217	0.149	0.196	0.515	0.256	0.097
33613	0.203	0.224	0.317	0.193	0.502	0.227	0.302
33614	0.146	0.13	0.941	0.085	0.973	0.177	0.366
33615	0.214	0.205	0.564	0.191	0.582	0.27	0.129
33616	0.138	0.128	0.802	0.131	0.555	0.167	0.257
35029	0.053	0.1	< 0.01	0.08	0.329	0.145	0.057
35030	0.134	0.136	0.406	0.098	0.797	0.217	0.111
35032	0.096	0.151	< 0.01	0.133	0.231	0.261	< 0.001

Table 5.3. Observed and expected encounter rate (encounters per 100 fixes) with wolves for 18 GPS-collared elk. Original wolf trajectories combined periods of low (~6 hours) and high (~1 hour) fix frequency, whilst standardised trajectories were characterised by a constant 1-hour fix frequency. The expected value represents the mean of a null distribution generated by randomly rotating the observed elk trajectory around its centre of gravity (Rotation Model), rotating and shifting the centre of gravity to a randomly selected relocation in the observed trajectory (RSH Model), and randomly sampling the distributions of step lengths and turning angles derived from the observed trajectory to construct a new correlated random walk (CRW Model). Shaded cells indicate elk showing an encounter rate with wolves that was lower than expected (one-tailed test, α = 0.05).

	Original wolf trajectories								Standardised wolf trajectories							
Elk ID	# encounters	Observed	Rotation Model		RSH Model		CRW Model		# encounters	Observed	Rotation Model		RSH Model		CRW Model	
			Expected	*P*	Expected	*P*	Expected	*P*			Expected	*P*	Expected	*P*	Expected	*P*
32298	6	0.348	0.452	0.248	0.37	0.604	0.453	0.426	8	0.764	0.629	0.981	0.594	0.634	0.708	0.411
32299	3	0.173	0.26	0.406	0.301	0.406	0.339	0.414	4	0.530	0.382	0.989	0.459	0.515	0.47	0.567
32300	4	0.230	0.191	0.693	0.349	0.515	0.337	0.419	4	0.530	0.202	0.634	0.565	0.475	0.518	0.455
32302	7	0.403	0.378	0.991	0.076	1.000	0.037	1.000	8	0.461	0.393	0.061	0.101	1.000	0.059	0.992
32312	5	0.380	0.359	0.644	0.091	0.972	0.2	0.882	12	0.912	0.763	0.277	0.199	0.991	0.41	0.930
32313	0	0.000	0.128	0.356	0.087	0.543	0.141	0.293	0	0.000	0.283	0.046	0.177	0.435	0.298	0.091
32315	5	0.297	0.419	0.322	0.473	0.247	0.457	0.433	6	0.356	0.524	0.792	0.808	0.198	0.74	0.277
32408	7	0.530	0.744	0.208	0.248	0.931	0.232	0.939	10	0.756	1.4	1.000	0.523	0.726	0.529	0.780
33609	3	0.177	0.093	1.000	0.06	0.992	0.105	0.828	3	0.177	0.108	0.752	0.119	0.816	0.195	0.632
33610	4	0.232	0.173	0.924	0.287	0.617	0.318	0.458	10	0.880	0.391	0.272	0.492	0.773	0.558	0.777
33611	4	0.238	0.252	0.663	0.353	0.539	0.406	0.364	12	0.713	0.522	0.721	0.567	0.724	0.712	0.683
33613	2	0.115	0.602	0.087	0.341	0.225	0.39	0.186	9	0.519	0.917	0.636	0.601	0.414	0.547	0.545
33614	2	0.115	0.086	0.930	0.084	0.861	0.088	0.812	4	0.230	0.204	0.364	0.146	0.792	0.172	0.792
33615	8	0.448	0.474	0.609	0.358	0.607	0.363	0.725	16	0.897	0.825	0.188	0.678	0.742	0.654	0.772
33616	1	0.069	0.099	0.614	0.11	0.560	0.214	0.451	1	0.069	0.156	0.832	0.222	0.333	0.354	0.257
35029	0	0.000	0.029	0.654	0.077	0.514	0.092	0.456	0	0.000	0.181	0.465	0.142	0.494	0.201	0.233
35030	5	0.372	0.26	0.844	0.148	0.941	0.188	0.899	9	0.670	0.431	0.423	0.272	0.905	0.411	0.842
35032	0	0.000	0.199	0.325	0.151	0.288	0.269	0.183	1	0.074	0.232	0.637	0.333	0.326	0.544	0.072

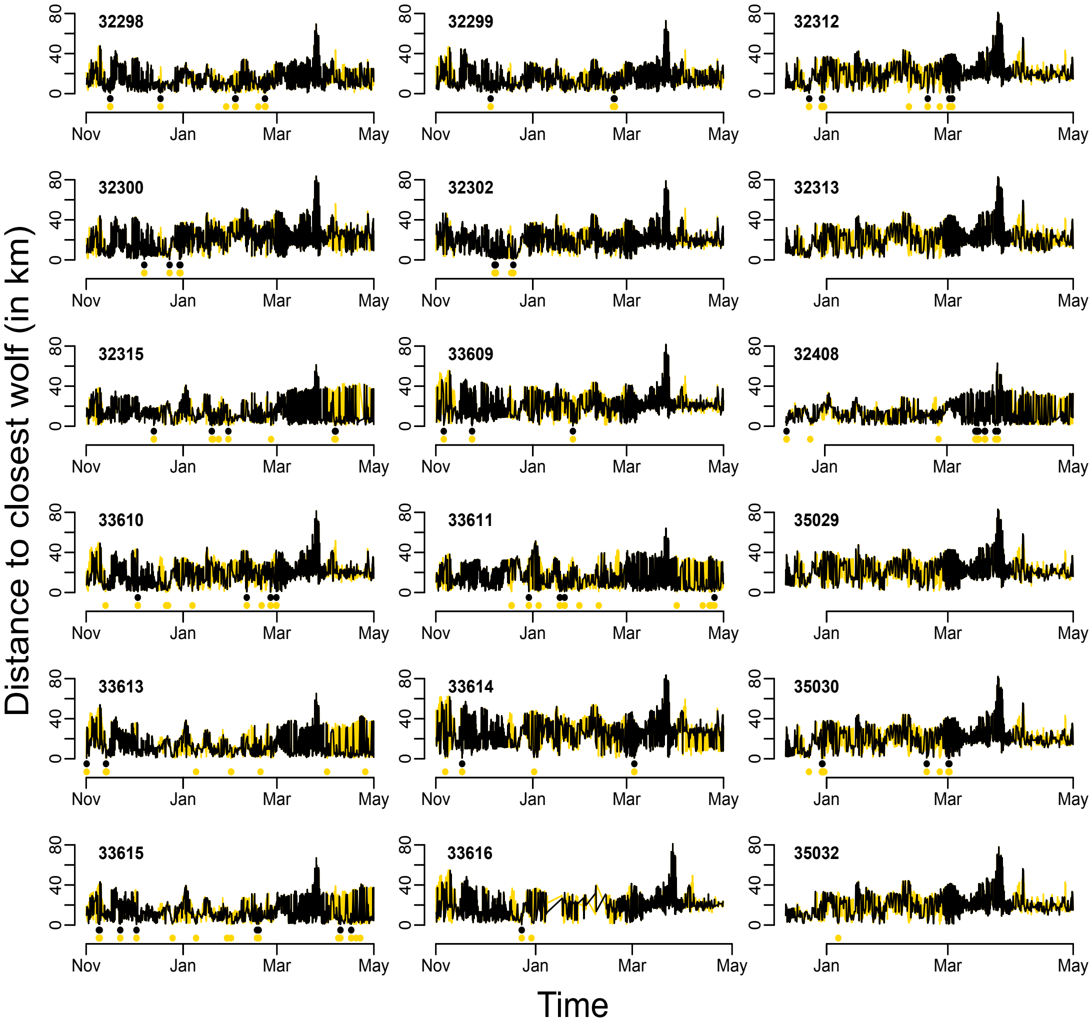

Figure 5.2. Time series of distance to the closest wolf for each elk considered in this study. Distance was calculated between relocations occurring within the same 1-hour window, with instances of close proximity (i.e. < 1000 m) denoted by full circles just above the x-axis. Black and yellow features represent distances and encounter events based on original wolf trajectories, which combined periods of low (~ 6 hours) and high (~ 1 hour) fix frequency, and those based on standardised wolf trajectories (fix frequency = 1 hour), respectively. Standardising wolf fix frequency to 1 hour tended to result in more encounter events.

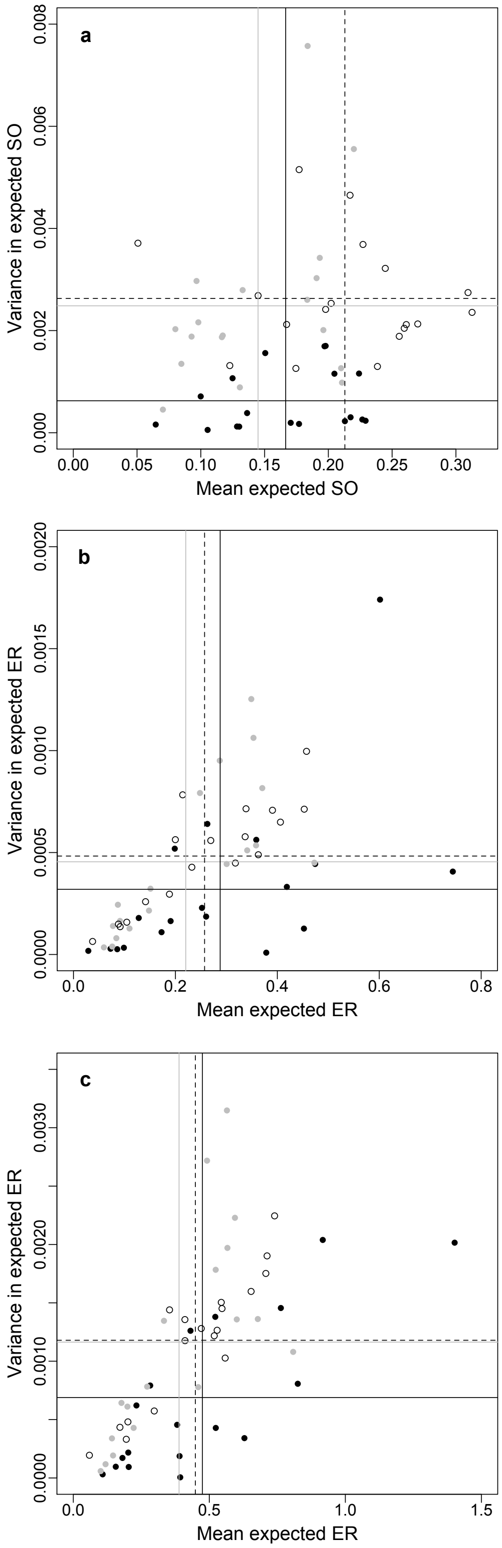

Figure 5.3. Mean and variance of expected distributions for (**a**) spatial overlap, and encounter rate (encounters per 100 elk fixes) based on (**b**) original and (**c**) standardised wolf trajectories. Null expectations were generated from the Rotation (full black circles and lines), RSH (full grey circles and grey lines) and CRW (open circles and dashed lines) models for each elk. Horizontal and vertical lines indicate the mean of each sample.

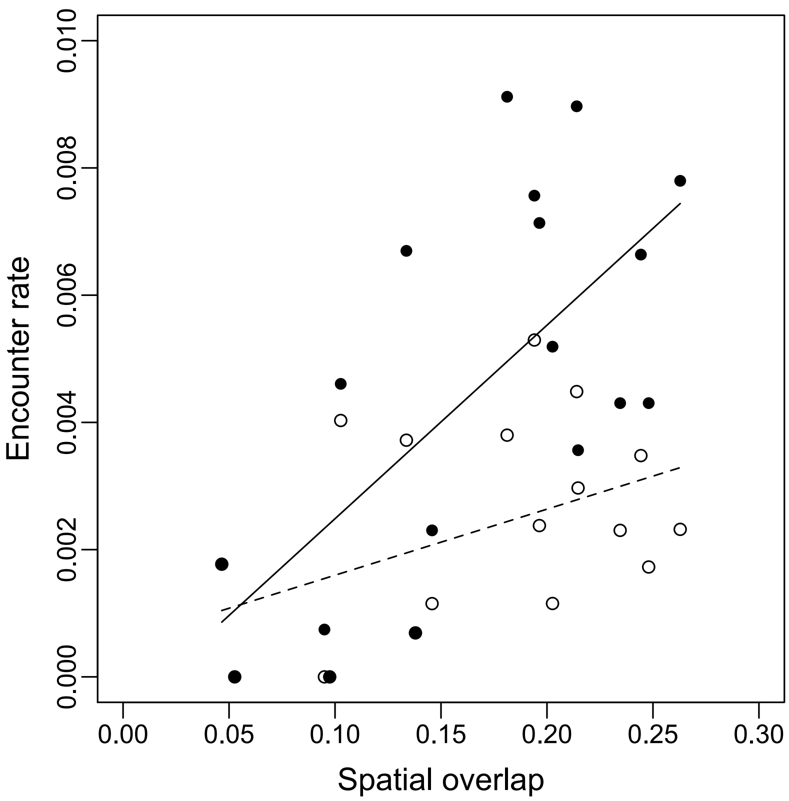

Figure 5.4. Encounter rate as a function of spatial overlap. Encounter rate was measured as the number of encounters per elk relocation (every 2.5 hours), and was derived from original (open circles) and standardised (full circles) wolf trajectories. Original wolf trajectories combined periods of low (~ 6 hours) and high (~ 1 hour) fix frequency whilst standardised trajectories were characterised by a constant 1-hour fix frequency. The dashed and full lines denote linear regression models (original trajectories: $R^2 = 0.11$, df = 16, $P < 0.05$; standardised trajectories: $R^2 = 0.42$, df = 16, $P < 0.001$). Encounter rate showed a linear relationship with spatial overlap, which was stronger when encounter rates were based on standardised wolf trajectories.

DISCUSSION

We estimated spatial overlap and encounter rates between GPS-collared elk and wolves in Northern YNP, and tested whether these were significantly lower than expectations based on three null model formulations. Our aim in doing this was to characterise spatial mechanisms of predator avoidance operating over long (i.e. proactive) and short (i.e. reactive) temporal scales. Overall, our analysis revealed an absence of significant avoidance behaviour – both proactive and reactive – for the majority of elk considered. Those individuals that did show a significantly lower spatial overlap than expected were not consistent across null models, highlighting the potential sensitivity of the approach to model formulation. Lastly, although standardising wolf fix frequency to 1 hour tended to increase observed encounter rates, it had a negligible effect on whether elk were perceived to actively minimise instances of close proximity.

Although the use of null models is widespread in community ecology (Gotelli & Graves 1996, O'Sullivan & Perry 2013), very few studies have applied them to infer on the interactive behaviour occurring between different species. Recently, Richard et al. (2013) revealed an overall absence of spatial segregation between female red and roe deer, but noted that outcomes varied depending on the null model formulation used to generate null trajectories. In a similar way, the models implemented in the present study led to expected distributions that differed in their mean and variance, though this rarely affected the random outcome found for the majority of collared elk. However, refining null model choice is clearly paramount to making conclusive inferences, and the fact that significant outcomes were never consistent across null models attests to this. In particular, null models in this study likely differed in the extent to which they allowed null trajectories to occupy a given geographic locality, with the RSH and CRW models producing trajectories over a wider area in comparison to the Rotation model. This may be particularly important for individual elk with a large proportion of relocations situated just outside of the joint wolf UD (i.e. low observed spatial overlap), which were generally the ones most likely to show significantly less spatial overlap with wolves than expected. Although our models could have incorporated processes such as the habitat preferences or state-dependent movement behaviours of elk (Morales et al. 2004, Hebblewhite et al. 2005), doing so could have resulted in the simulated trajectories being too similar to the observed, thus reducing statistical power (the Narcissus effect; Wilson 1995). Moreover, such information is not always readily available, and in this respect, our study is of value in highlighting the challenges associated with testing hypotheses relating to species interactions when prior information on animal behaviour is limited.

Nevertheless, the observed lack of response by elk to the distribution of wolves concurs with findings from previous research carried out in Northern YNP. In their study of elk movement patterns before and after wolf reintroduction, Mao et al. (2005) found that elk "did not spatially separate themselves from wolves" during winter months. Rather, the availability of suitable forage, snow depth and habitat type were found to be more important factors determining elk movements (Fortin et al. 2005, White and

Garrott 2005, 2012). In this context, our study provides further evidence that wolf distribution (or density) at the landscape-level may be a poor indicator of predation risk. Kauffman et al. (2007) highlighted a discrepancy between kill site occurrence and wolf distribution, which in our case, suggests elk might have been responding to the former rather than the latter. Furthermore, elk are unlikely to be aware of the spatial distribution of a predator known to frequently, but unpredictably, course throughout their winter range (Bergman et al. 2006, Kauffman et al. 2007). Instead, they may select for landscape features that reduce their vulnerability to being hunted, such as increased vegetation cover (Creel et al. 2005, Fortin et al. 2005) or proximity to roads (Nelson et al. 2012).

Few studies have investigated the spatial – as opposed to the behavioural (e.g. vigilance) – responses of elk to wolf movement at fine spatial scales. Recently, Middleton et al. (2013) showed that elk tended to increase their rates of movement and displacement when wolves were within a distance threshold of 1 km, but that such behaviour was relatively infrequent and that its strength varied considerably across individual elk. The latter study was heavily criticised for under-estimating the frequency of wolf-elk encounters due to step and scatter biases (see Creel et al. 2013). However, our study suggests that, although encounter rates may be under-estimated as a result of predator fix frequency, this does not necessarily change the random nature of elk behaviour with reference to wolf movement. The latter trend was supported by a stronger linear relationship between spatial overlap and encounter rate, which would be expected if elk did not balance the risk of sharing more space with predators by being more responsive to their immediate presence (Lima & Bednekoff 1999, Creel et al. 2008). Other studies have also highlighted that factors such as elk group size (Gower et al. 2008, White et al. 2012), switches in habitat use (Creel et al. 2005, Fortin et al. 2005, Hernández and Laundré 2005), and wolf pack size (MacNulty et al. 2011) may allow elk to minimise predation risk despite close proximity to wolves, thus dampening spatial avoidance patterns.

We must acknowledge the limitations of our study. Firstly, the 2.5-hour frequency used to record elk movement trajectories – which we did not correct for – may have led us to overlook instances of close proximity with wolves, and even entire hunting episodes (MacNulty 2002, MacNulty et al. 2007). Secondly, standardised wolf trajectories were generated using the same process as that used to estimate the joint wolf UD, which may have increased the likelihood of obtaining a stronger linear relationship between spatial overlap and encounter rate. Future studies should consider alternative ways of generating additional wolf relocations (e.g. kinematic movement approach, Long 2015). Furthermore, although our study considers movement trajectories from members of the dominant packs in the NR, we recognise that the fission-fusion nature of wolf societies may have exacerbated the under-estimation of encounter rates. More generally, the encounter rate considered in this study is a point-based measure of potential interaction, meaning that the GPS data are conceptualised as discrete locations at which individuals occur. Alternative path-based measures, which typically consider the cohesiveness in movement trajectories (i.e. similar or dissimilar step lengths and turning angles), represent another potential way of assessing the responses of elk to wolves. Ultimately, however, both point and path based measures are relatively uninformative unless compared to values obtained under the assumption that two individuals move randomly with reference to each other (Miller 2015). In this respect, the recent development of coupled step selection functions that enable quantification of the effects of habitat and heterospecifics on movement decisions represents a promising avenue for future research (Potts et al. 2014).

In summary, our study emphasises the challenges of making inferences on the nature of anti-predator responses displayed by prey from spatial data alone. Whilst our analyses focus on two methodological aspects, namely null model choice and fix frequency, other ecological factors such as habitat type, or characteristics of the individual prey such as vigilance levels or body condition, may interact to blur intricate spatial responses. Although our data were based on a system that has undergone extensive study over the past two decades, the considerations we highlight are particularly relevant to telemetry studies carried out in poorly known landscapes, in which spatial data are increasingly the first to be collected. In such cases, a clear understanding of species interactions, such as the proactive and reactive responses of prey to predators considered in this study, may have to be gained through a combination of GPS telemetry and other field-based methods (e.g. direct observation, camera trapping).

ACKNOWLEDGEMENTS

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SUPPORTING INFORMATION

Figure S5.1. Distributions of movement correlation and average distance between simultaneous relocations across elk dyads.

Figure S5.2. Time series of distance between simultaneous relocations for wolf dyads.

Figure S5.3. Probability density function of the expected distribution of spatial overlap for each elk.

Figure S5.4. Probability density function of the expected distribution of encounter rate for each elk (original wolf trajectories).

Figure S5.5. Probability density function of the expected distribution of encounter rate for each elk (standardised wolf trajectories).

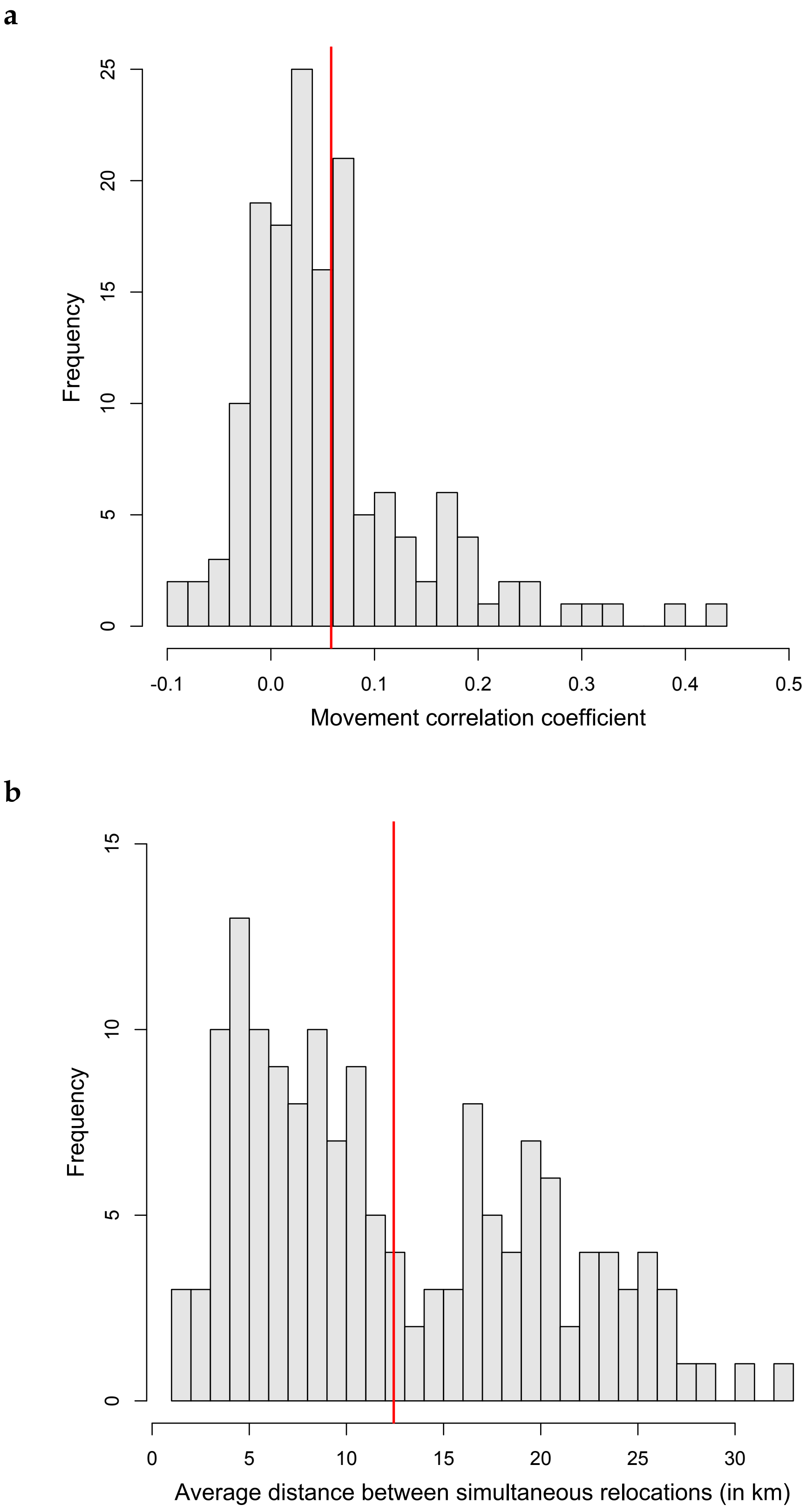

Figure S5.1. Distribution of movement correlation (**a**) and average distance between simultaneous relocations (**b**) across elk dyads (vertical red lines indicate distribution means).

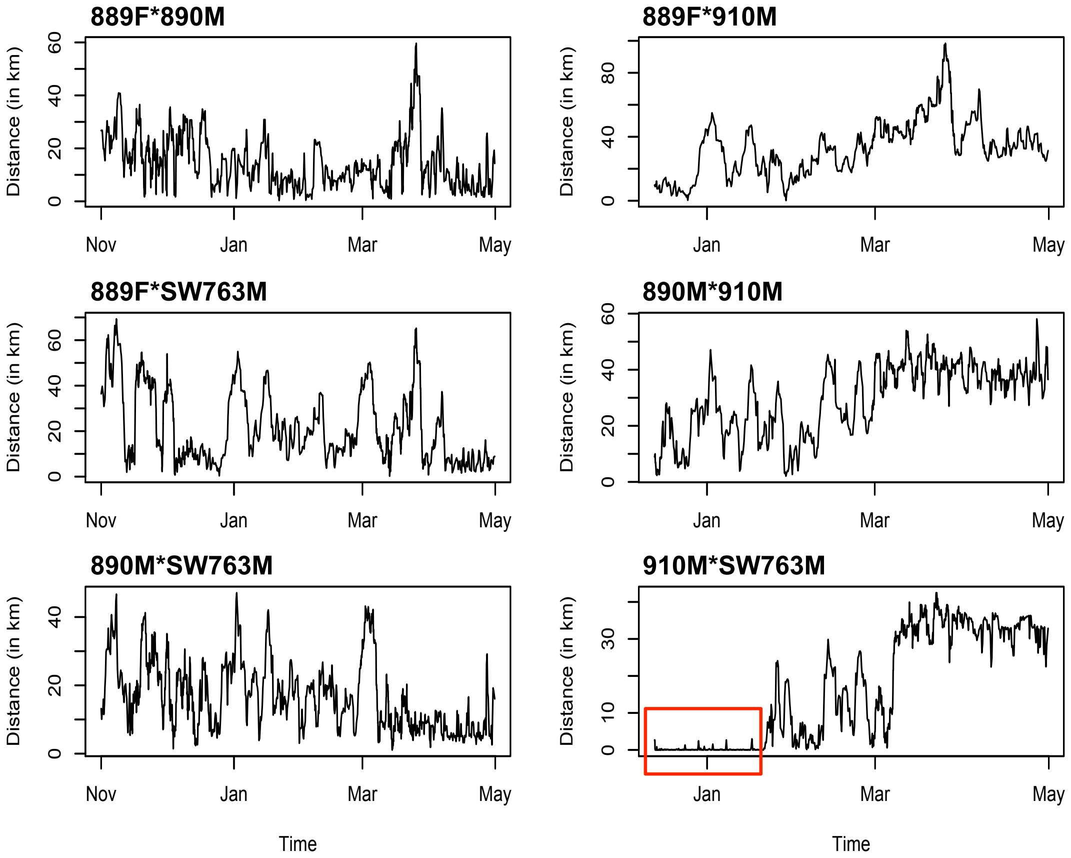

Figure S5.2. Time series of distance between simultaneous relocations for wolf dyads. The red box indicates a period of joint movement exhibited by individuals 910M and SW763M.

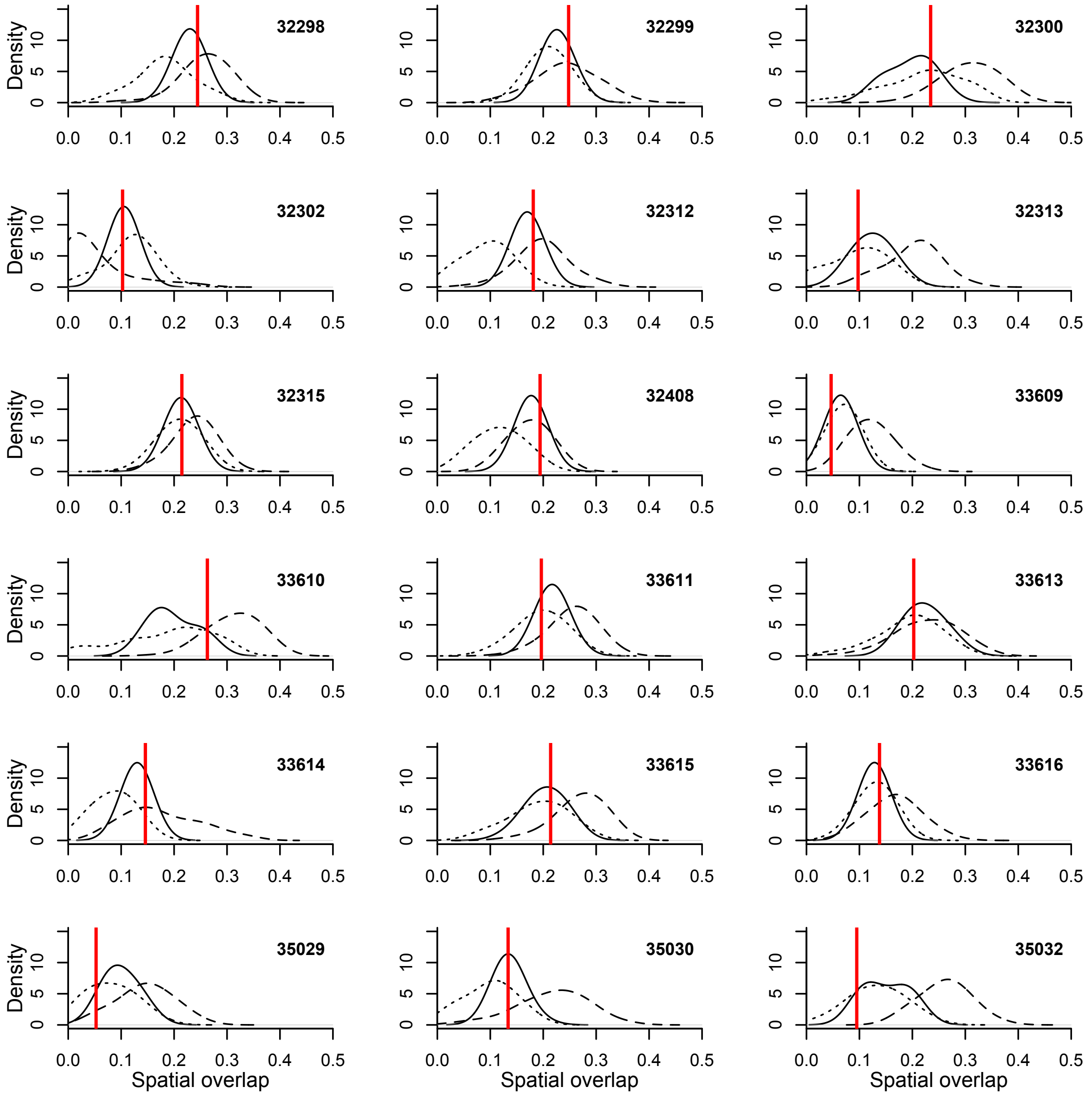

Figure S5.3. Probability density function of the expected distribution of spatial overlap for each elk, generated from three different null model formulations: Rotation (full line), RSH (dashed line) and CRW (dotted line). The red vertical line indicates the observed level of spatial overlap with wolves.

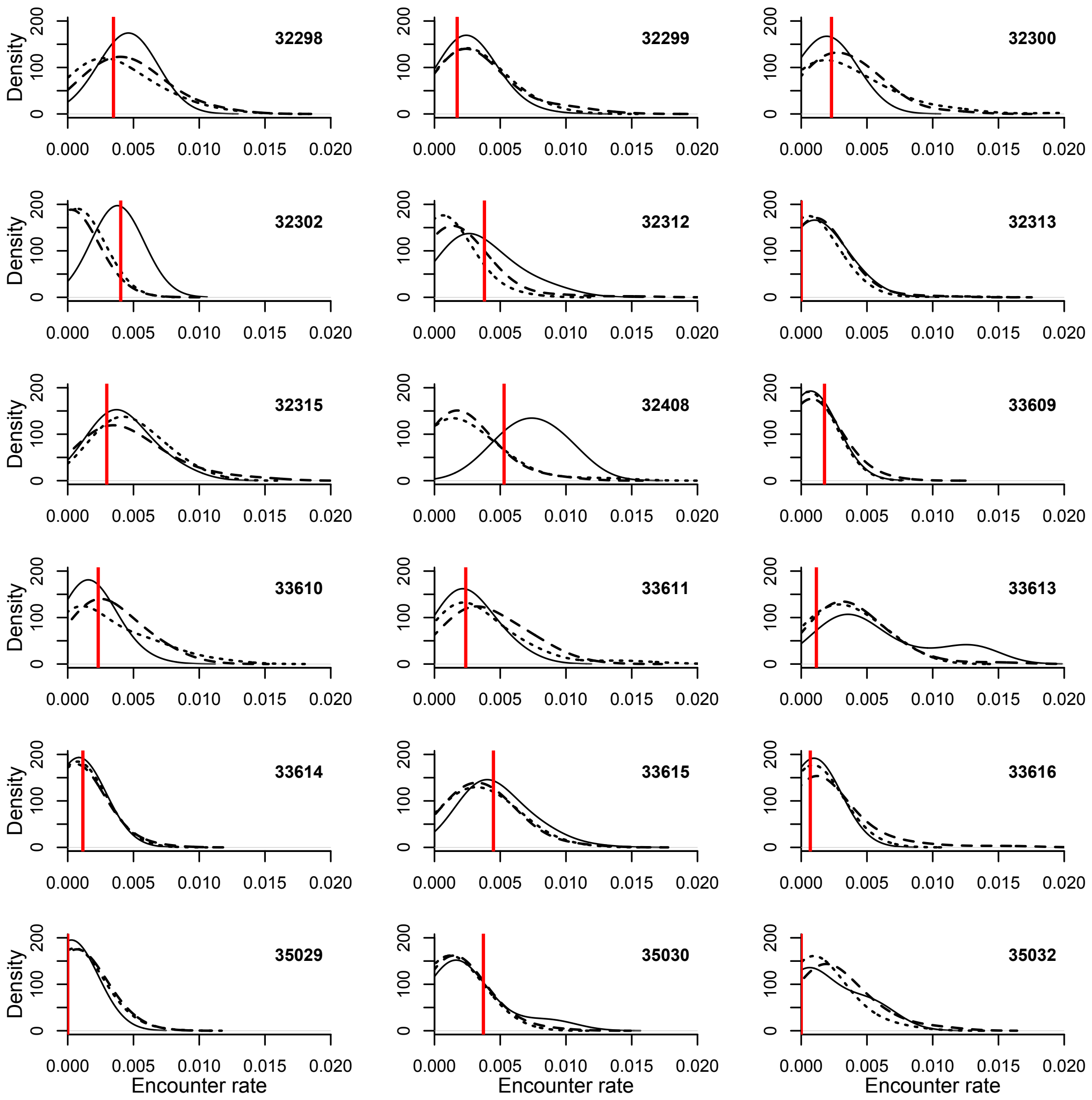

Figure S5.4. Probability density function of the expected distribution of encounter rate for each elk, generated from three different null model formulations: Rotation (full line), RSH (dashed line) and CRW (dotted line). Encounter rate was based on original wolf trajectories, which combine periods of high (~1 hour) and low (~6 hour) fix frequency. The red vertical line indicates the observed level of spatial overlap with wolves.

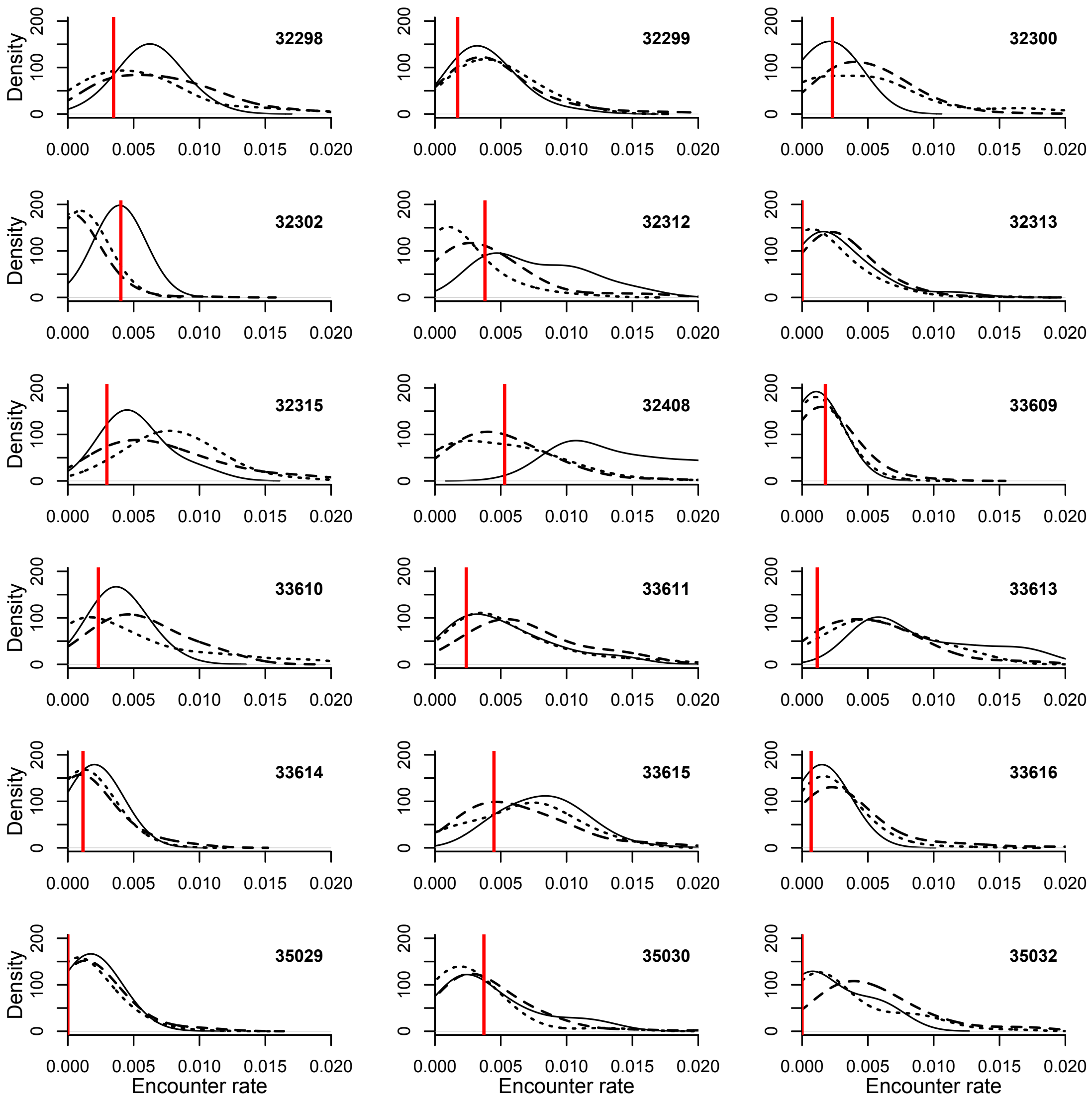

Figure S5.5. Probability density function of the expected distribution of encounter rate for each elk, generated from three different null model formulations: Rotation (full line), RSH (dashed line) and CRW (dotted line). Encounter rate was based on standardised wolf trajectories, which were characterised by a constant 1-hour fix frequency. The red vertical line indicates the observed level of spatial overlap with wolves.

REFERENCES

Barasona, J. A., M. C. Latham, P. Acevedo, J. A. Armenteros, A. D. M. Latham, C. Gortazar, F. Carro, R. C. Soriguer, and J. Vicente (2014). Spatiotemporal interactions between wild boar and cattle: implications for cross-species disease transmission. *Veterinary Research* **45**, 122.

Basille, M., D. Fortin, C. Dussault, G. Bastille-Rousseau, J. P. Ouellet, and R. Courtois (2015). Plastic response of fearful prey to the spatiotemporal dynamics of predator distribution. *Ecology* **96**, 2622–2631.

Benhamou, S., M. Valeix, S. Chamaillé-Jammes, D. W. Macdonald, and A. J. Loveridge (2014). Movement-based analysis of interactions in African lions. *Animal Behaviour* **90**, 171–180.

Benson, J. F., and B. R. Patterson (2015). Spatial overlap, proximity, and habitat use of individual wolves within the same packs. *Wildlife Society Bulletin* **39**, 31–40.

Bergman, E. J., R. A. Garrott, S. Creel, J. J. Borkowski, R. Jaffe, and F. G. R. Watson (2006). Assessment of prey vulnerability through analysis of wolf movements and kill sites. *Ecological Applications* **16**, 273–284.

Bhattacharyya, A. (1943). On some sets of sufficient conditions leading to the normal bivariate distribution. *Sankhyā: The Indian Journal of Statistics* **6**, 399-406.

Broekhuis, F., G. Cozzi, M. Valeix, J. W. McNutt, and D. W. Macdonald (2013). Risk avoidance in sympatric large carnivores: reactive or predictive? *Journal of Animal Ecology* **82**, 1098–1105.

Brough, A. M. (2009). *Summer home range fidelity in adult female elk (*Cervus elaphus*) in northwestern Colorado* Thesis. Utah State University, Logan, USA.

Bullard, F. (1999). *Estimating the home range of an animal: a Brownian bridge approach* Thesis. University of North Carolina, Chapel Hill, USA.

Calenge, C. (2006). The package "adehabitat" for the R software: a tool for the analysis of space and habitat use by animals. *Ecological Modelling* **197**, 516–519.

Courbin, N., D. Fortin, C. Dussault, V. Fargeot, and R. Courtois (2013). Multi-trophic resource selection function enlightens the behavioural game between wolves and their prey. *Journal of Animal Ecology* **82**, 1062–1071.

Courbin, N., A. J. Loveridge, D. W. Macdonald, H. Fritz, M. Valeix, E. T. Makuwe, and S. Chamaillé-Jammes (2015). Reactive responses of zebras to lion encounters shape their predator–prey space game at large scale. *Oikos*, DOI: 10.1111/oik.02555.

Creel, S., J. Winnie Jr, B. Maxwell, K. Hamlin, and M. Creel (2005). Elk alter habitat selection as an antipredator response to wolves. *Ecology* **86**, 3387–3397.

Creel, S., J. A. Winnie, D. Christianson, and S. Liley (2008). Time and space in general models of antipredator response: tests with wolves and elk. *Animal Behaviour* **76**, 1139–1146.

Creel, S., J. A. Winnie, and D. Christianson (2013). Underestimating the frequency, strength and cost of antipredator responses with data from

GPS collars: an example with wolves and elk. *Ecology and Evolution* **3**, 5189–5200.

Despain, D. G. (1990). *Yellowstone vegetation: consequences of environment and history in a natural setting*. Roberts Rinehart Publishers.

Doncaster, C. P. (1990). Non-parametric estimates of interaction from radio-tracking data. *Journal of Theoretical Biology* **143**, 431–443.

Fieberg, J. (2007). Kernel density estimators of home range: smoothing and the autocorrelation red herring. *Ecology* **88**, 1059–1066.

Fieberg, J., and C. O. Kochanny (2005). Quantifying home-range overlap: the importance of the utilization distribution. *The Journal of Wildlife Management* **69**, 1346–1359.

Fortin, D., H. L. Beyer, M. S. Boyce, D. W. Smith, T. Duchesne, and J. S. Mao (2005). Wolves influence elk movements: behavior shapes a trophic cascade in Yellowstone National Park. *Ecology* **86**, 1320–1330.

Gotelli, N. J. (2000). Null model analysis of species co-occurrence patterns. *Ecology* **81**, 2606–2621.

Gotelli, N. J., and G. R. Graves (1996). *Null models in ecology*. Smithsonian Institution Press, Washington D. C.

Gower, C. N., R. A. Garrott, P. J. White, F. G. Watson, S. S. Cornish, and M. S. Becker (2008). Spatial responses of elk to wolf predation risk: using the landscape to balance multiple demands. *Terrestrial Ecology* **3**, 373–399.

Hebblewhite, M., E. H. Merrill, and T. L. McDonald (2005). Spatial decomposition of predation risk using resource selection functions: an example in a wolf–elk predator–prey system. *Oikos* **111**, 101–111.

Hernández, L., and J. W. Laundré (2005). Foraging in the 'landscape of fear' and its implications for habitat use and diet quality of elk *Cervus elaphus* and bison *Bison bison*. *Wildlife Biology* **11**, 215–220.

Horne, J. S., E. O. Garton, S. M. Krone, and J. S. Lewis (2007). Analyzing animal movements using Brownian bridges. *Ecology* **88**, 2354–2363.

Houston, D. G. (1982). *The northern Yellowstone elk: ecology and management.* Macmillan Publishing, New York.

Kauffman, M. J., N. Varley, D. W. Smith, D. R. Stahler, D. R. MacNulty, and M. S. Boyce (2007). Landscape heterogeneity shapes predation in a newly restored predator–prey system. *Ecology Letters* **10**, 690–700.

Kays, R., M. C. Crofoot, W. Jetz, and M. Wikelski (2015). Terrestrial animal tracking as an eye on life and planet. *Science* **348**, DOI: 10.1126/science.aaa2478

Kernohan, B. J., R. A. Gitzen, and J. J.Millspaugh (2001). Analysis of animal space use and movements. In *Radiotracking and animal populations*, pp. 125–166. Academic, San Diego.

Latombe, G., D. Fortin, and L. Parrott (2014). Spatio-temporal dynamics in the response of woodland caribou and moose to the passage of grey wolf. *Journal of Animal Ecology* **83**, 185–198.

Laundré, J. W., L. Hernández, and K. B. Altendorf (2001). Wolves, elk, and bison: reestablishing the" landscape of fear" in Yellowstone National Park, USA. *Canadian Journal of Zoology* **79**, 1401–1409.

Laundré, J. W. (2010). Behavioral response races, predator-prey shell games, ecology of fear, and patch use of pumas and their ungulate prey. *Ecology* **91**, 2995–3007.

Liley, S., and S. Creel (2008). What best explains vigilance in elk: characteristics of prey, predators, or the environment? *Behavioral Ecology* **19**, 245–254.

Lima, S. L., and P. A. Bednekoff (1999). Temporal variation in danger drives antipredator behavior: the predation risk allocation hypothesis. *The American Naturalist* **153**, 649–659.

Lima, S. L., and L. M. Dill (1990). Behavioral decisions made under the risk of predation: a review and prospectus. *Canadian Journal of Zoology* **68**, 619–640.

Long, J. A., T. A. Nelson, S. L. Webb, and K. L. Gee (2014). A critical examination of indices of dynamic interaction for wildlife telemetry studies. *Journal of Animal Ecology* **83**, 1216–1233.

Long, J. A. (2015). Kinematic interpolation of movement data. *International Journal of Geographical Information Science* **30**, 854–868.

Lührs, M. L., and P. M. Kappeler (2013). Simultaneous GPS tracking reveals male associations in a solitary carnivore. *Behavioral Ecology and Sociobiology* **67**, 1731–1743.

Macdonald, D. W., F. G. Ball, and N. G. Hough (1980). The evaluation of home range size and configuration using radio-tracking data. In *A handbook on biotelemetry and radio tracking*, pp. 405-424. Pergamon Press, Oxford.

MacNulty, D. R. (2002). *The predatory sequence and the influence of injury risk on hunting behavior in the wolf* Thesis. University of Minnesota, Minneapolis and St. Paul.

MacNulty, D. R., L. D. Mech, and D. W. Smith (2007). A proposed ethogram of large-carnivore predatory behavior, exemplified by the wolf. *Journal of Mammalogy* **88**, 595–605.

MacNulty, D. R., D. W. Smith, L. D. Mech, J. A. Vucetich, and C. Packer (2011). Nonlinear effects of group size on the success of wolves hunting elk. *Behavioral Ecology*, DOI: 10.1093/beheco.arr159.

Mao, J. S., M. S. Boyce, D. W. Smith, F. J. Singer, D. J. Vales, J. M. Vore, and E. H. Merrill (2005). Habitat selection by elk before and after wolf reintroduction in Yellowstone National Park. *The Journal of Wildlife Management* **69**, 1691–1707.

Middleton, A. D., M. J. Kauffman, D. E. McWhirter, J. G. Cook, R. C. Cook, A. A. Nelson, M. D. Jimenez, and R. W. Klaver (2013). Animal migration amid shifting patterns of phenology and predation: lessons from a Yellowstone elk herd. *Ecology* **94**, 1245–1256.

Miller, J. A. (2015). Towards a better understanding of dynamic interaction metrics for wildlife: a null model approach. *Transactions in GIS* **19**, 342–

361.

Millspaugh, J. J., R. A. Gitzen, B. J. Kernohan, M. A. Larson, and C. L. Clay (2004). Comparability of three analytical techniques to assess joint space use. *Wildlife Society Bulletin* **32**, 148–157.

Morales, J. M., D. T. Haydon, J. Frair, K. E. Holsinger, and J. M. Fryxell (2004). Extracting more out of relocation data: building movement models as mixtures of random walks. *Ecology* **85**, 2436–2445.

Nelson, A. A., M. J. Kauffman, A. D. Middleton, M. D. Jimenez, D. E. McWhirter, J. Barber, and K. Gerow (2012). Elk migration patterns and human activity influence wolf habitat use in the Greater Yellowstone Ecosystem. *Ecological Applications* **22**, 2293–2307.

O'Sullivan, D., and G. L. Perry (Eds.) (2013). *Spatial simulation: exploring pattern and process*. John Wiley & Sons.

Pianka, E. R. (1986). *Ecology and natural history of desert lizards: analyses of the ecological niche and community structure*. Princeton University Press, Princeton.

Potts, J. R., K. Mokross, and M. A. Lewis (2014). A unifying framework for quantifying the nature of animal interactions. *Journal of The Royal Society Interface*, DOI: 10.1098/rsif.2014.0333.

Proffitt, K. M., J. Grigg, K. Hamlin, and R. A. Garrott (2009). Contrasting effects of wolves and human hunters on elk behavioural responses to predation risk. *The Journal of Wildlife Management* **73**, 345–356.

Proffitt, K. M., P. J. White, and R. A. Garrott (2010). Spatio-temporal overlap between Yellowstone bison and elk–implications of wolf restoration and other factors for brucellosis transmission risk. *Journal of Applied Ecology* **47**, 281–289.

R Development Core Team (2015). R: a language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. www.rproject.org

Richard, E., C. Calenge, S. Saïd, J. Hamann, and J. M. Gaillard (2013). Studying spatial interactions between sympatric populations of large herbivores: a null model approach. *Ecography* **36**, 157–165.

Robert, K., D. Garant, and F. Pelletier (2012). Keep in touch: does spatial overlap correlate with contact rate frequency? *The Journal of Wildlife Management* **76**, 1670–1675.

Searle, K. R., C. J. Stokes, and I. J. Gordon (2008). When foraging and fear meet: using foraging hierarchies to inform assessments of landscapes of fear. *Behavioral Ecology* **19**, 475–482.

Shirabe, T. (2006). Correlation analysis of discrete motions. In *GIScience: Lecture Notes in Computer Science* **4197**, 370–82. Springer-Verlag, Berlin.

Sih, A. (1984). The behavioural response race between predator and prey. *The American Naturalist* **123**, 143–150.

Sih, A. (1998). Game theory and predator–prey response races. In *Game theory and animal behaviour*, pp. 221–238. Oxford University Press, Oxford.

Smith, D. W., D. R. Stahler, E. Stahler, M. Metz, K. Quimby, R. McIntyre, C. Ruhl, and M. McDevitt (2014). *Yellowstone National Park wolf project annual report 2013.* National Park Service, Yellowstone Center for Resources, Yellowstone National Park, Wyoming, USA.

Smith, D. W., D. R. Stahler, E. Stahler, M. Metz, K. Cassidy, B. Cassidy, and R. McIntyre (2015). *Yellowstone National Park wolf project annual report 2014.* National Park Service, Yellowstone Center for Resources, Yellowstone National Park, Wyoming, USA.

Thaker, M., A. T. Vanak, C. R. Owen, M. B. Ogden, S. M. Niemann, and R. Slotow (2011). Minimizing predation risk in a landscape of multiple predators: effects on the spatial distribution of African ungulates. *Ecology* **92**, 398–407.

Valeix, M., A. J. Loveridge, S. Chamaillé-Jammes, Z. Davidson, F. Murindagomo, H. Fritz, and D. W. Macdonald (2009). Behavioral adjustments of African herbivores to predation risk by lions: spatiotemporal variations influence habitat use. *Ecology* **90**, 23–30.

Walrath, R., T. R. Van Deelen, and K. C. VerCauteren (2011). Efficacy of proximity loggers for detection of contacts between maternal pairs of white-tailed deer. *Wildlife Society Bulletin* **35**, 452–460.

Weissburg, M., D. L. Smee, and M. C. Ferner (2014). The sensory ecology of nonconsumptive predator effects. *The American Naturalist* **184**, 141–57.

White, P. J., and R. A. Garrott (2005). Northern Yellowstone elk after wolf restoration. *Wildlife Society Bulletin* **33**, 942–955.

White, P. J., K. M. Proffitt, and T. O. Lemke (2012). Changes in elk distribution and group sizes after wolf restoration. *The American Midland Naturalist* **167**, 174–187.

Williams, D. M., A. C. D. Quinn, and W. F. Porter (2014). Informing disease models with temporal and spatial contact structure among GPS-collared individuals in wild populations. *PLoS One* **9**, e84368.

Wilson, J. B. (1995). Null models for assembly rules: the Jack Horner effect is more insidious than the Narcissus effect. *Oikos* **72**, 139–144.

Chapter 6

Camera traps offer limited potential for inferring on the spatial responses of prey to predators: a simulation study based on wolf-elk behaviour

- Running head -

Simulating camera trap sampling of predator-prey movements

- Title -

Camera traps offer limited potential for inferring on the spatial responses of prey to predators: a simulation study based on wolf-elk behaviour

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ABSTRACT

We used a simulation approach based on the well-known predator-prey interaction occurring between wolves (*Canis lupus*) and elk (*Cervus elaphus*) in Yellowstone's Northern Range to assess whether predator avoidance strategies operating at different spatiotemporal scales could be inferred from camera trap data. Specifically, we consider a proactive response whereby elk avoid areas in which they are more likely to encounter wolves (the risky places hypothesis, RPH), and two reactive responses corresponding to the risky times (RTH; elk respond to temporal variation in risk) and the risk allocation (RAH; elk respond to both temporal and spatial variation in risk) hypotheses. We assess whether each of these scenarios could produce distinct spatial and spatiotemporal patterns in camera trapping data collected using 4 different levels of effort (50, 100, 200 and 400 cameras deployed across the NR). We find that, on average, spatial and spatiotemporal patterns resulting from the RPH and the RTH, respectively, could be distinguished from patterns produced under random movement rules. At lower levels of camera trapping effort (i.e. 50 and 100 cameras), however, the RTH and RAH yielded spatial patterns that were no different to those derived from random movement rules. Random permutation of elk records at the level of each scenario iteration demonstrated low potential as a method for inferring avoidance behaviour from a single camera trap survey. Our simulation approach, whilst simple in many respects, highlights the challenges of inferring reactive response behaviour from camera trap data.

INTRODUCTION

Camera trap surveys are increasingly being used to study the spatiotemporal behaviour of predators and prey (Harmsen et al. 2011, Lazenby and Dickman 2013, Ross et al. 2013, Bischof et al. 2014). Although such surveys are typically restricted to a finite set of spatial locations (i.e. individual camera placements; Cusack et al. 2015), they provide spatiotemporal occurrence data on multiple sympatric species in a way that is largely non-invasive to individual animals (Rovero et al. 2013). Moreover, as passive sensors, camera traps have the potential to sample a larger number of individuals from a given population (Kays et al. 2009), and may thus facilitate the generalisation of observed interactive behaviour at the population- or species-level (O'Connell et al. 2010). This is in contrast to global positioning satellite (GPS) telemetry, which typically targets only a small subset of individuals from any given population, and rarely individuals belonging to both predator and prey populations. With the increasing popularity of camera trap surveys worldwide, there is a pressing need to evaluate whether the data generated from these can reliably and efficiently be used to characterise often-complex interactive behaviours associated with predator-prey interactions.

The spatiotemporal response of prey to the presence of predators is an important component of predator-prey interactions (Sih 1984, 1998, Thaker et al. 2011, Weissberg et al. 2014). Predator avoidance can occur over large spatial scales (several kilometres), with prey proactively avoiding areas where the long-term risk of predation is high (Creel et al. 2008), a theory commonly described as the risky places hypothesis (RPH). The latter relies on the existence of a heterogeneous landscape of predation risk, with clear refugia characterised by a lower probability of encountering predators (Laundré et al. 2001, Laundré 2010, Searle et al. 2008). Alternatively, prey may respond reactively, but consistently, to the presence of one or several predators in their immediate surroundings. Under the risky times hypothesis (RTH), prey response is characterised by increased movement rates and displacement distances away from perceived contemporaneous and/or recent predator locations in the immediate vicinity (Caro 2005, Proffitt et al. 2009, Rogala et al. 2011, Middleton et al 2013, Basille et al. 2015, Courbin et al. 2015). Finally, the strength of reactive responses may vary depending on the level of long-term risk experienced in a given area (Lima and Bednekoff 1999). The risk allocation hypothesis (RAH) states that prey should spend more time carrying out risky activities, such as foraging, when the background level of risk is high. In other words, prey should display less pronounced reactive movement behaviour to the immediate presence of predators in areas where the latter are often encountered (Creel et al. 2008).

Patterns indicative of the RPH have been highlighted in past camera trap studies investigating species responses to predators or competitors. For example, Muhly et al. (2011) showed that prey species in south-western Alberta, Canada, were more likely to use camera trap sites characterised by high human activity, and consequently less predator activity. Similarly, Kays et al. (2015) revealed coyote spatial activity to be a strong negative predictor of that of domestic cats in the eastern United States. In contrast, few camera trap studies have focused on RTH and RAH-type response mechanisms. This may be due to the challenges involved in quantifying reactive behaviours occurring over very short spatial and temporal scales, for which a high level of camera trapping effort is likely required. Despite this, Cusack et al. (in review; see Chapter 4) recently proposed a method to quantify the temporal spacing between captures of predators and prey at shared camera trap locations. They fall short, however, of providing a method to test whether the observed pattern is significantly different to that expected based on a null model assuming no avoidance by prey.

In this study, we assess whether distinct predator avoidance strategies operating at different spatiotemporal scales can be inferred from camera trap data collected using arrays of different camera densities. We consider the well-known predator-prey interaction occurring between wolves (*Canis lupus*) and elk (*Cervus elaphus*) in Yellowstone National Park (YNP). In this system, the RPH, RTH and RAH all represent plausible predator avoidance mechanisms implemented by elk (Creel et al. 2008), which are the primary prey of wolves and constitute up to 92% of kills during the winter months (Smith et al. 2004). Most studies up until now have relied on field observations and GPS collar data to infer on elk responses to wolf movement, but none have considered the use of camera traps to investigate these behaviours. Field trials are costly to undertake, however, and in this study we use individual-based models (IBMs) to simulate the movement of wolf packs and elk groups across YNP's Northern Range (NR) according to all three avoidance scenarios and one random movement control scenario. Individual based-models can be used to input a simple set of rules into the movement of multiple interacting agents (e.g. elk and wolves) in order to produce population-level patterns (DeAngelis et al. 1994). The latter can then be sampled to test a wide range of monitoring methods and associated analytical tools in a way that would be too costly to perform empirically (Grimm 1999, Grimm et al. 2006). We render our simulations more realistic by basing wolf and elk movement parameters on two-state hidden Markov models (HMMs) fitted to GPS collar data collected on both species in YNP's NR. We then simulate the deployment of camera trap arrays of varying density (i.e. varying effort) across the entire NR, and assess whether each prey response scenario can be distinguished from the resulting spatiotemporal patterns.

METHODS

Wolf and elk movement parameters

We fitted one- and two-state hidden Markov models (HMMs) to pooled wolf (n=3) and elk (n=12) GPS collar data collected between 14th November and 15th December 2013 in YNP's NR. During this period, wolf collars emitted one relocation every hour (mean = 1.03, SD = 0.36) whilst elk collars emitted on average once every 2.5 hours (mean 2.48, SD = 0.40). For both species, we assumed a Weibull distribution for the step lengths, and a wrapped Cauchy distribution for the turning angles (Langrock et al. 2012). The Weibull distribution is defined by shape and scale parameters ($k > 0$ and $\lambda > 0$, respectively) and the wrapped Cauchy distribution by its mean and concentration ($-\pi < \mu < \pi$ and $0 < \rho < 1$, respectively). Starting values for parameter estimation were based on 100 model iterations with starting values chosen between 0 and 2 for step length parameters, and between –π and π for turning angle parameters. Final starting values were taken as the respective means of the resulting distributions. Hidden Markov models were parameterised using the R package moveHMM (Michelot et al. 2016), with parameters estimated via numerical maximum likelihood (Langrock et al. 2012). For each species, one- and two-state models were compared based on their AIC. We assessed the goodness-of-fit of the selected model by computing the quantile residuals, also known as pseudo-residuals. As a general rule, if the model is the true data-generating process, the pseudo-residuals should follow a normal distribution (Zucchini and Macdonald 2009, Langrock et al. 2012).

Simulating predator avoidance scenarios

Using parameters from selected HMMs, we simulated the movement of 4 wolf packs and 150 elk groups across YNP's NR according to three plausible anti-predator response scenarios (RPH, RTH and RAH) and one random control (Random). All trajectories were composed of 2,160 hourly relocations, representing 90 days of movement. In all cases, we first generated wolf pack trajectories across the NR and estimated their joint utilisation distribution (UD) by applying a fixed kernel across pooled relocations (Calenge 2006). The value of the smoothing parameter was set to the reference bandwidth using the function *kernelUD* in the R package adehabitatHR (Calenge 2006). From the resulting joint UD we derived the 50% contour isopleth, which was subsequently used to define areas of high use by wolves (i.e. core territories).

We derived an estimate of the number of elk groups by dividing the total number of elk counted in the NR in 2013 (3,915 individuals; YNP unpublished data) by the mean group size (~26 individuals; YNP unpublished data). We further assumed elk groups moved independently from one another and distributed their activity evenly across the entire NR.

To implement the RPH simulation, we produced elk trajectories that remained in a "commuting" state when within the 50% contour isopleth of the joint wolf UD (i.e. high probability of encountering a predator). In other words, simulated elk trajectories did not display foraging behaviour when in areas of high predator use, and thus tended to travel faster through these. The latter behaviour likely represented a much more realistic approximation of spatial avoidance than complete avoidance of wolf core territories. For the RTH, elk movement was biased away from any wolf relocation occurring during the past 24 hours within a distance threshold of 1 km (following Middleton et al. 2013). This scenario was thus expected to result in an absence of elk detections within the 24 hours following detection of a wolf. Finally, in the RAH simulation, elk response to nearby wolf relocations was dependent on its position within the joint wolf UD. If the elk location was outside of the estimated 50% contour isopleth, movement in close proximity to wolves followed the same rules as in the RTH scenario. If, on the other hand, the elk location was within wolf core territory, movement was biased away from contemporaneous wolf relocations (i.e. those occurring during the same or previous time step) only. Biased movement by elk was implemented by shifting the mean of the turning angle distribution to the opposite heading to that of the closest contemporaneous wolf position. The R code used to implement simulations can be found in Code S6.1.

Camera trap surveys

We carried out 100 iterations per scenario, each of these sampled with 4 levels of camera trapping effort. The latter consisted of 50, 100, 200 and 400 camera traps deployed in a systematic way across the entire NR, corresponding to densities of roughly 0.033, 0.067, 0.133 and 0.267 cameras per km2 (Figure 6.1). For a given level of effort, the location of camera traps was held constant across scenarios and iterations. For simplicity, camera traps were assumed to have a circular detection area of radius 100 m. Although this value is unrealistic, it enabled us to account for increased detection probability of a group of elk or pack of wolves relative to the solitary agents in our simulations. Thus, wolf and elk detections by camera traps were each characterised by a specific time step and location.

Data analysis

We extracted two simple metrics from the simulated camera trap data. The first measured the spatial overlap (SO) between elk and wolves as

$$\mathrm{SO} = \sum_{k=1}^{K} \min\,(p_{wolf,k} p_{elk,k})$$

in which $p_{wolf,k}$ and $p_{elk,k}$ are the proportional usages of camera trap k by wolves and elk, respectively. Note that, for a given species, the sum of p_k across all K camera traps is equal to 1. The SO index therefore ranges from 0 (no shared use of camera trap sites) to 1 (complete overlap in the use of camera trap sites). The second metric was the probability of obtaining at least one elk detection within the 24 hours following the detection of a wolf, which we refer to as the follow-up probability (FUP). For a given scenario iteration, FUP was estimated as n_{elk}/N where N is the total number of independent wolf detections and n_{elk} is the number of these for which at least 1 elk detection was obtained in the following 24 hours. Note that if another wolf detection was obtained before an elk within 24 hours, or if a wolf detection occurred less than 24 hours before the end of the survey, the resulting binomial trial was not used to estimate the FUP.

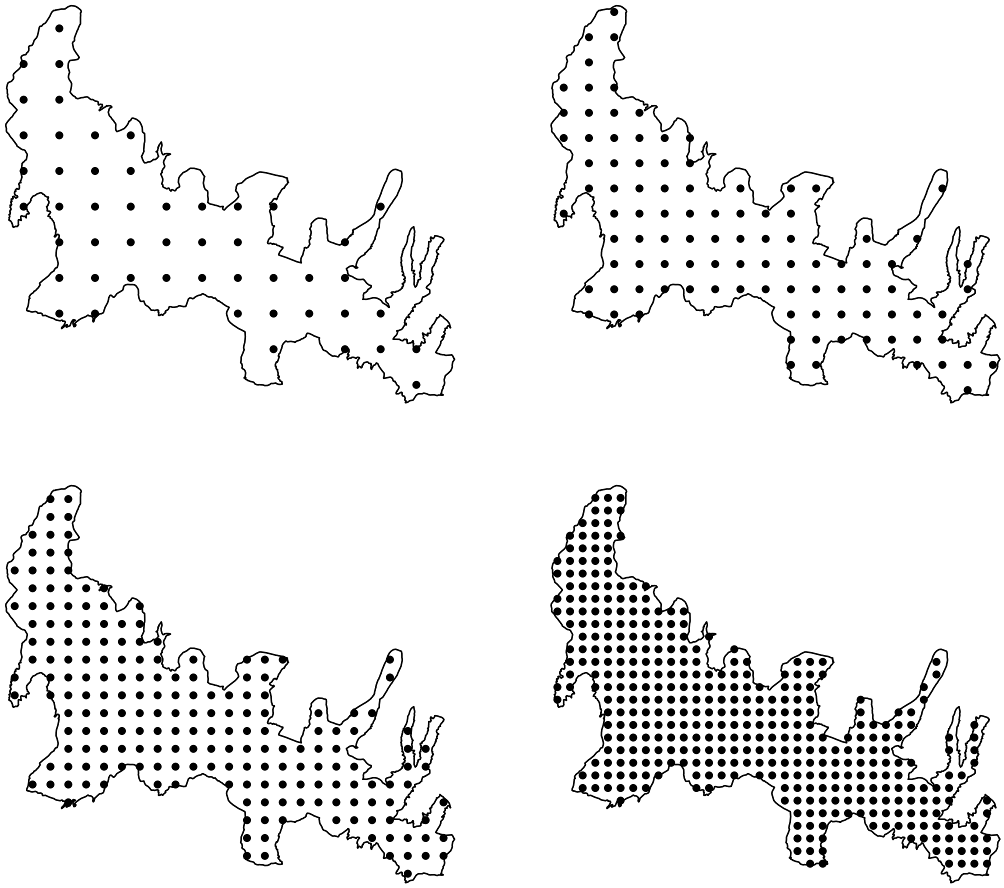

Figure 6.1. Camera trap surveys simulated in this study. The number of camera traps deployed across Yellowstone National Park's Northern Range (black boundary) ranged from 50 (top left) to 400 (bottom right).

For a given level of camera trapping effort, we implemented a one-way ANOVA to compare mean values of SO. Prior to doing this we tested for homogeneity of variances using Bartlett's K-squared test. To compare FUP across scenarios, we modelled the proportion of successes (i.e. n_{elk}) versus failures (i.e. $N - n_{elk}$) as a function of scenario type using a quasi-binomial GLM with a logit link function. In both cases, we measure the significance of the effect of each avoidance scenario relative to the Random scenario.

We were also interested in measuring to what extent patterns obtained at the level of each scenario iteration could be used to infer on the underlying avoidance behaviour of elk. For this a null model was required to generate a detection pattern across camera traps that would be expected under the null hypothesis of random movement of elk. In the present study, we permuted elk capture records across all camera locations, all the while keeping associated time steps unchanged. The latter model enabled us to retain the same distribution of captures per camera, as well as the serially correlated nature of elk detections. Indeed, the latter tended to occur in clumps, a pattern that is commonly encountered when a group of herbivores forages in front of a camera trap for several consecutive hours. As an aside, we note that elk capture records could have also been shifted forward or backward by a random number of time steps (see Benhamou et al. 2014 for a similar method applied to telemetry data). In our case, however, doing this had no influence on the resulting null distribution of either SO or FUP.

We carried out 1,000 null permutations per scenario iteration, re-calculating both metrics with the unmodified distribution of wolf records. In both cases, we derived the probability of the null hypothesis being true as the proportion of permutations yielding values that were smaller or equal to the observed (Gotelli and Graves 1996, Dufrêne and Lengendre 1997). We chose to implement a one-tailed test based on a α level of 0.05, as we were interested in the alternative hypothesis of avoidance. All simulations and analyses were carried out in R version 3.2.1 (R Core Development Team 2015).

RESULTS

Wolf and elk movement parameters

A two-state hidden Markov model applied to pooled elk trajectories outperformed a model assuming no state-dependent process ($AIC_{1\text{-state}}$ = 9365.5 versus $AIC_{2\text{-state}}$ = 9196.8). In contrast, wolf movement was best modelled as a single-state correlated random walk ($AIC_{1\text{-state}}$ = 4720.9 versus $AIC_{2\text{-state}}$ = 6740.7). Elk movement was found to switch between a state characterized by lower speeds and more diffuse turning angles, and a state characterized by higher speeds and a narrower turning angle distribution (Table 6.1; see Figure S6.1 for goodness-of-fit test results). Although wolf trajectories reflected more wide-ranging movement behaviour (Table 6.1), it must be noted that collared individuals showed a propensity for sharp turns, which contributed towards decreasing model goodness-of-fit (Figure S6.2).

Camera trapping simulations

For both wolves and elk, the total number of detections increased significantly with camera trapping effort in all scenarios (Table 6.2). Detection rates for elk were marginally lower in the RTH and RAH scenarios, whilst those for wolves were consistent across scenarios. One-way ANOVAs indicated significant variation in SO across scenarios at all levels of camera trapping effort (Table 6.3). The variance explained by the model was 18.4 % when 50 cameras were used, 32.2 % for 100 cameras, 47.4 % for 200 cameras, and 57.7 % for 400 cameras (see Table 6.3 for corresponding R^2 values). Across all levels of effort, the RPH scenario was characterised by average values of SO that were significantly lower than those recorded for the Random scenario (Figure 6.2; see Table 6.3 for results of statistical comparisons across scenarios). Similarly, the RTH and RAH scenarios resulted in mean FUPs that were significantly lower than the Random scenario, regardless of camera trapping effort. A significant difference in mean SO was only noted for the RTH scenario when 200 and 400 camera traps were deployed across the NR. At no level of camera trapping effort was mean SO from the RAH scenario different to that obtained from the Random scenario. Finally, all scenarios were characterised by a significantly lower mean FUP when 200 and 400 cameras were used. It must be noted that distributions of FUP showed a general tendency to be zero-inflated (Figure 6.2). Despite the use of quasi-binomial GLMs, the level of overdispersion remained high (scale parameters: $\varphi_{50} = 1.3$, $\varphi_{100} = 1.5$, $\varphi_{200} = 1.7$, $\varphi_{400} = 1.8$).

The proportion of iterations resulting in lower than expected SO, as inferred from our random permutation test, increased with sampling effort for all scenarios except the Random one (Figure 6.3). In the latter case, increasing effort resulted in a lower proportion of iterations yielding a measure of SO that was statistically different from random, thus reducing the likelihood of producing a Type 1 error. In contrast, only 26 % of RPH scenario iterations yielded patterns that were distinguished as non-random when 50 cameras were used, versus 50, 62 and 70 % when 100, 200 and 400 cameras were deployed, respectively (Table 6.3). Thus, even when considerable camera trapping effort was implemented, there was still a 24 % chance of not inferring proactive avoidance behaviour by elk as simulated in the RPH scenario (i.e. committing a Type 2 error). Although proactive avoidance was not simulated as part of the RTH and RAH, a small proportion of iterations of these scenarios resulted in non-random SO (Figure 6.3). These proportions tended to be higher than those obtained for the Random scenario, indicating that they were likely not the result of chance. Rather, RTH and RAH scenarios could indirectly result in lower than expected SO.

Table 6.1. Estimated parameters for step length and turning angle distributions derived from two-state hidden Markov models applied to pooled elk and wolf relocations in the Northern Range of YNP.

Species	State	Speed (Weibull)		Turning angle (wrapped Cauchy)		Probability of transitioning to other state
		Shape	Scale	Mean	Concentration	
Elk	1	0.809	0.343	0.058	0.057	0.134
	2	0.789	0.135	0.057	0.414	0.076
Wolf	1	0.857	0.856	0.012	0.258	-

In contrast, our permutation test rarely enabled us to infer on the reactive behaviour of elk at the level of each simulation. For levels of effort involving 50 and 100 cameras deployed across the NR, we recorded 100 % of Type 2 errors for all avoidance scenarios. Only when 200 and 400 cameras were deployed did permutation tests have enough power to detect non-random patterns in the detection data resulting from the RTH and RAH scenarios. However, even then, only a small proportion of iterations resulted in lower than expected FUP (Figure 6.3).

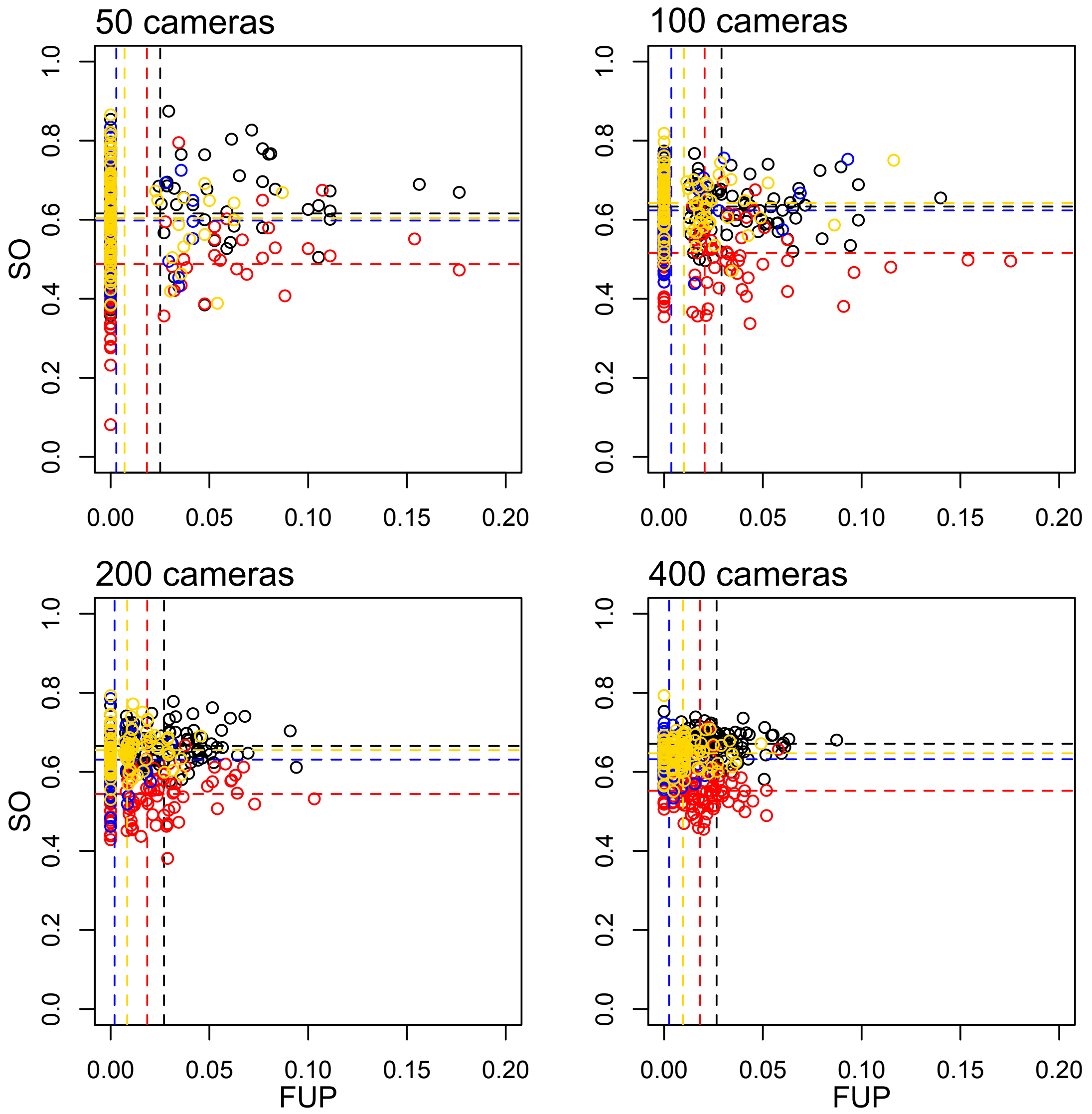

Figure 6.2. Spatial overlap (SO) and follow-up probability (FUP) values derived from camera trap data collected on simulated wolf and elk trajectories. The latter were generated according to three avoidance scenarios (RPH, red; RTH, blue; and RAH, gold), as well as a control scenario based on random movement rules (black). Each plot relates to a different level of camera trapping effort, defined as the number of camera traps deployed in a systematic fashion across Yellowstone National Park's Northern Range. Dashed lines denote mean values of SO (horizontal) and FUP (vertical). The variation in SO values explained by a one-way ANOVA increased with the level of effort (see text for values).

Table 6.2. Mean number of elk and wolf detections recorded for each simulated scenario and level of camera trapping effort.

Camera effort	Scenario	# Elk detections		# Wolf detections	
		Mean	SD	Mean	SD
50	Random	495.6	76.5	25	7.1
	RPH	463.7	93.6	25.7	7.6
	RTH	426.9	88.8	25.9	6.7
	RAH	510.3	98.6	25.2	7.1
100	Random	1029.1	125.2	51.2	10.4
	RPH	951	141.8	52.7	11.8
	RTH	935.3	133.4	53.5	9.7
	RAH	1006.9	153.2	52.7	10.8
200	Random	2029.5	177.6	102.1	13.8
	RPH	1917.4	220.2	102.6	13.3
	RTH	1836.8	207	104.3	15.3
	RAH	2050.1	207.7	106	13.9
400	Random	4020.1	261.5	201.4	18.4
	RPH	3725.9	324.2	200.6	18.3
	RTH	3559.1	240.8	209.7	21.3
	RAH	4009.7	292.6	206.1	21.9

Table 6.3. Results of statistical tests used to compare average levels of spatial overlap (SO) and follow-up probability (FUP) across scenarios for each level of camera trapping effort. For each model, estimates for the mean SO and FUP obtained for the RPH, RTH and RAH are compared to the corresponding means obtained for the Random scenario. In the case of one-way ANOVAs, we give the R^2 value, which quantifies the amount of variance explained by the model. For quasi-binomial GLMs, we present the over-dispersion parameter φ. Shaded cells represent significant differences relative to Random scenario estimates.

Camera		SO (One-way ANOVA)			FUP (Quasi-binomial GLM)			
effort	Scenario	Mean	*t*-value	*P*	Estimate (Mean)	SE	*t*-value	*P*
50	Random	0.616	56.2	-	-3.694 (0.024)	0.144	-25.7	-
	RPH	0.488	47.9	< 0.001	-0.255 (0.019)	0.221	-26.854	0.249
	RTH	0.598	55.0	0.248	-2.101 (0.003)	0.427	-30.622	< 0.001
	RAH	0.604	55.5	0.457	-1.242 (0.007)	0.298	-29.865	< 0.001
	Model $R^2 = 0.184$				*Model* $\varphi = 1.3$			
100	Random	0.633	88.3	-	-3.518 (0.029)	0.118	-29.8	-
	RPH	0.516	76.7	< 0.001	-0.329 (0.021)	0.183	-31.595	0.0734
	RTH	0.623	87.3	0.334	-2.097 (0.004)	0.353	-35.74	< 0.001
	RAH	0.642	89.2	0.361	-1.065 (0.010)	0.232	-34.39	< 0.001
	Model $R^2 = 0.322$				*Model* $\varphi = 1.5$			
200	Random	0.666	128.8	-	-3.581 (0.027)	0.079	-45.6	-
	RPH	0.544	112.2	< 0.001	-0.386 (0.019)	0.124	-48.718	< 0.001
	RTH	0.631	124.1	< 0.001	-2.655 (0.002)	0.293	-54.647	< 0.001
	RAH	0.658	127.3	0.146	-1.208 (0.008)	0.159	-53.217	< 0.001
	Model $R^2 = 0.474$				*Model* $\varphi = 1.7$			
400	Random	0.671	174.7	-	-3.606 (0.027)	0.060	-60.1	-
	RPH	0.552	152.8	< 0.001	-0.386 (0.018)	0.094	-64.202	< 0.001
	RTH	0.632	167.5	< 0.001	-2.386 (0.003)	0.199	-72.082	< 0.001
	RAH	0.660	173.2	0.074	-1.054 (0.009)	0.116	-69.209	< 0.001
	Model $R^2 = 0.577$				*Model* $\varphi = 1.8$			

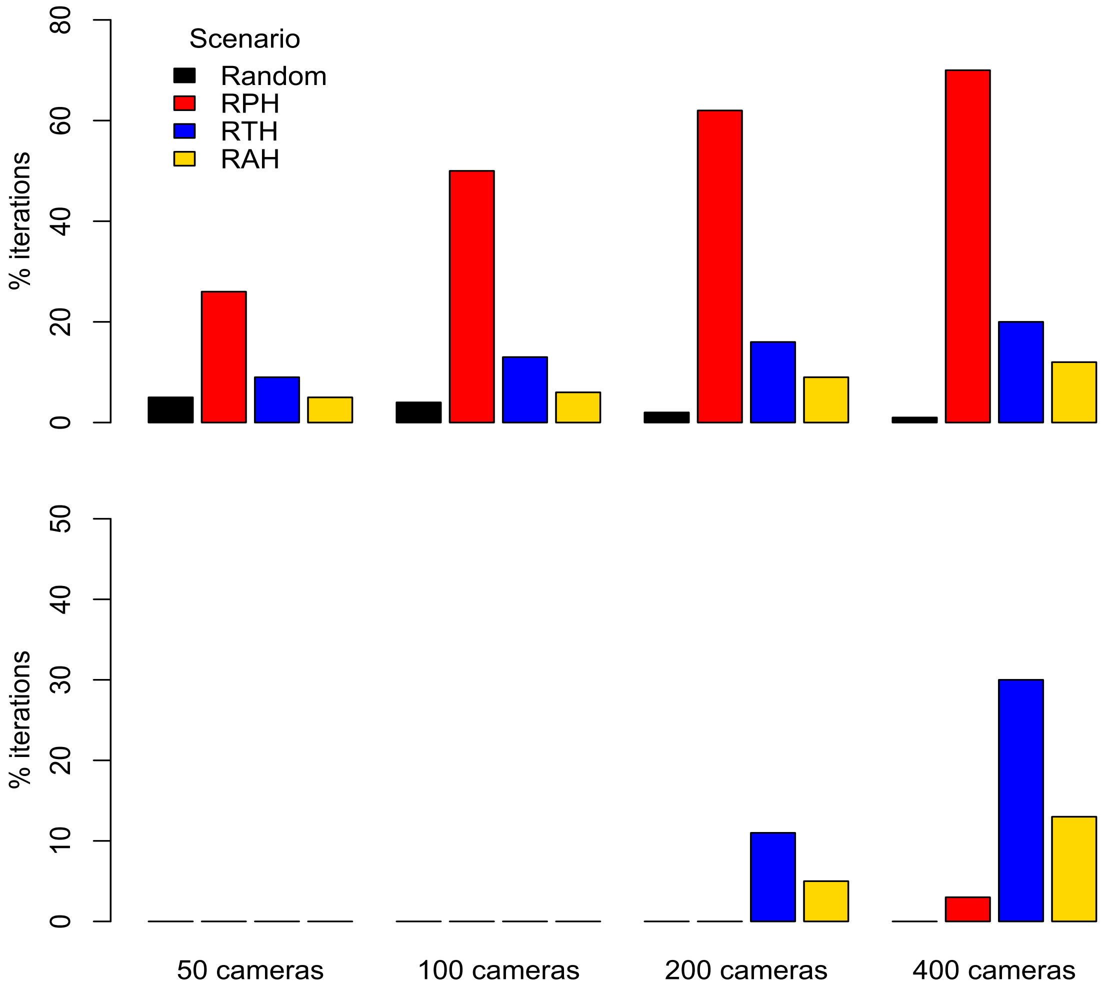

Figure 6.3. Percentage of iterations resulting in lower than expected SO (top) and FUP (bottom) for different avoidance scenarios and levels of camera trapping effort deployed across the NR. Statistical testing consisted in generating a null distribution by permuting elk records across camera trap sites and deriving the proportion of permutations yielding values that were smaller or equal to the observed. Note, y-axes vary.

DISCUSSION

This is the first study to implement an IBM framework to test the potential for inferring on the behavioural aspects of predator-prey interactions from camera trap data. In particular, our simulations incorporated key aspects of the wolf-elk predator-prey system. Firstly, the movement parameters on which we base the state-dependent trajectories of wolves and elk were in agreement with what is known of their biology. Morales et al. (2004) highlighted the bi-phasic movement behaviour of elk, with clear encamped and exploratory states. Wolf movement was reflective of their well-known cursorial behaviour, which enables them to cover long distances in search of prey (Mech and Boitani 2010). Secondly, all three avoidance scenarios simulated in this study reflected plausible responses of elk to wolf movement. Kauffman et al. (2007) showed that both wolf territoriality and habitat type could generate a heterogeneous risk landscape, with distinct hunting grounds and prey refugia that elk could respectively avoid and use to minimise predation, as per the RPH. In support of the RTH, Middleton et al. (2013) showed that elk tended to increase their rates of movement, displacement and vigilance when wolves were within a distance threshold of 1 km. Finally, Creel et al. (2008) and Basille et al. (2015) demonstrated that the strength of the response of elk and caribou to the nearby presence of wolves was dependent on the level of long-term risk, as predicted by the RAH.

Despite widespread evidence for reactive responses of prey to predators (Weissberg et al. 2014, Cooper and Blumstein 2015, Courbin et al. 2015), most camera trap studies consider avoidance as a purely spatial process, one that results in a clear segregation of long-term spatial activity. This is often the assumption underlying co-occupancy models, which are commonly used to assess whether the probability of camera site occupancy or use by a species is dependent on that of another (Mackenzie et al. 2004, Sollmann et al. 2012, Bischof et al. 2014). Our study highlights that segregation between predator and prey long-term spatial activities is indeed more likely to be detected than more intricate reactive behaviours occurring at finer spatiotemporal scales. However, we also show that failure to reveal a clear disassociation between the long-term spatial activities of two potentially interacting species does not imply a lack of avoidance behaviour. In particular, we find that reactive predator avoidance mechanisms displayed by elk, such as those implemented in the RTH and RAH scenarios, can yield spatial patterns that are no different to those derived from random movement rules. This was especially the case for levels of effort that are commonly encountered in the camera trapping literature, i.e. grids of 50 to 100 camera points (O'Connell et al. 2010). This finding supports the recommendations of Cusack et al. (in review; see Chapter 4) concerning the use of spatiotemporal approaches to infer interactive behaviours from camera trap data.

Estimating the probability of detecting an elk in the 24 hours following the detection of a wolf (i.e. the FUP) did help differentiate the RTH scenario from the Random one at all levels of camera trapping effort. While this is an encouraging result, our study also highlights the challenges of correctly inferring reactive behaviour from a single camera trap survey. Such surveys are typically only carried out once in a given area, signifying that a null expectation must often be generated based on the photographic data at hand. In this respect, our permutation approach and subsequent statistical testing offered limited potential for correct inferences to be drawn regarding elk avoidance behaviour, and especially at low levels of camera trapping effort. Lower effort generally resulted in higher variability in SO and FUP values – reflecting higher sampling error – which might have increased the likelihood of obtaining an observed pattern of photographic records that was closer to random. In the case of FUP, permutations of elk records often resulted in expected values of zero, thus forcing a lower bound on the resulting null distribution. This boundary was less likely at the highest level of camera trapping effort, which could explain why permutation tests associated with these were less likely to yield non-random outcomes. Finally, it is also possible that even the highest density of camera traps considered in this study was too low to detect reactive behaviour.

It is important to emphasise that our simulations represent simplified scenarios that do not include all potential behavioural processes involved in predator-prey interactions. For instance, all individuals within the simulated elk population displayed the same avoidance response to wolf movement, thus potentially over-representing the corresponding behaviour at the population level. This simplification was necessary in order to be able to clearly attribute population level patterns to a given predator avoidance strategy. However, we acknowledge it may not be entirely realistic. Recent studies have highlighted heterogeneity in elk response to wolf presence (Middleton et al. 2013, Creel et al. 2005), and more generally there have been calls for increased consideration of individual variability in predator-prey interactions (Pettorelli et al. 2015). Similarly, our simulations did not incorporate the biased movement of wolves towards prey at fine spatial scales (e.g. hunting). Lastly, the camera trap detection zone used in this study is likely to be unrealistic, even though it was chosen to account for the social behaviour of elk and wolves. In particular, it may not have been suitable to use the same detection zone for both species owing to the differences in both group size and movement speeds. True detection rates for wolves in particular are likely to be much lower than portrayed in this study, and we urge future studies to better account for the detection process in their simulations. Overall, however, rather than contradict our findings, all of these processes are likely to further blur both the spatial and temporal patterns associated with proactive and reactive prey responses, thus making it even harder to draw inferences from camera trap data.

As a final note, our study does not address the influence of camera trap survey design on the study of predator-prey interactions. For simplicity, we simulated the placement of camera traps as random across the entire NR, thus reflecting a large-scale approach (see Swanson et al. 2015 for a real-world example). Our reason for doing this was to highlight that despite a huge amount of camera trapping effort, characterising interactive behaviour from the location and timing of photographs is challenging. However, alternative survey designs may target specific habitats, or take on a more experimental approach whereby prey habitat preferences or vigilance levels – the latter estimated from camera trap images (e.g. Altendorf et al. 2001, Hernández et al. 2005, Le Saout et al. 2015) – are compared between areas in which predators are known to be present or absent. Alternatively, recent studies have attempted to reveal temporal segregation between predators and their prey by comparing activity patterns of the latter in the presence and absence of the former (Ross et al. 2013, Tambling et al. 2015). Such designs may enable more robust inferences to be made on the response of prey to predators.

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SUPPORTING INFORMATION

Code S6.1 – R code to run prey response scenarios – see https://github.com/jeremycusack/Prey_spatial_response_models

Figure S6.1 – Description of movement states obtained by fitting a hidden Markov model to pooled elk trajectories.

Figure S6.2 - Description of the single movement state obtained by fitting a hidden Markov model to pooled wolf trajectories.

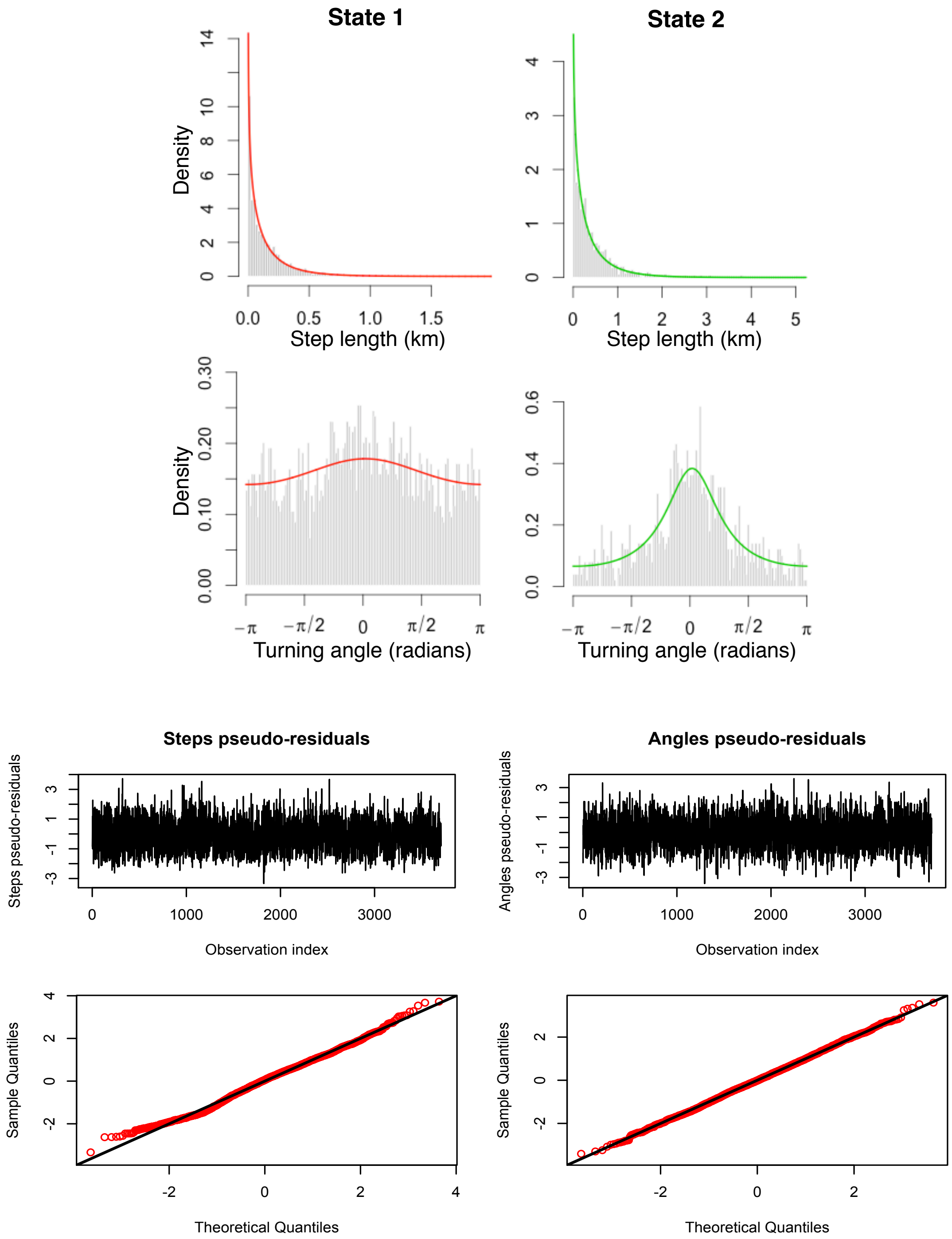

Figure S6.1. Step length and turning angle distributions (top plots) associated with the two-state movement of elk, as estimated from a hidden Markov model implemented in the R package moveHMM. Bottom plots show pseudo-residuals and normality diagnostic graphs.

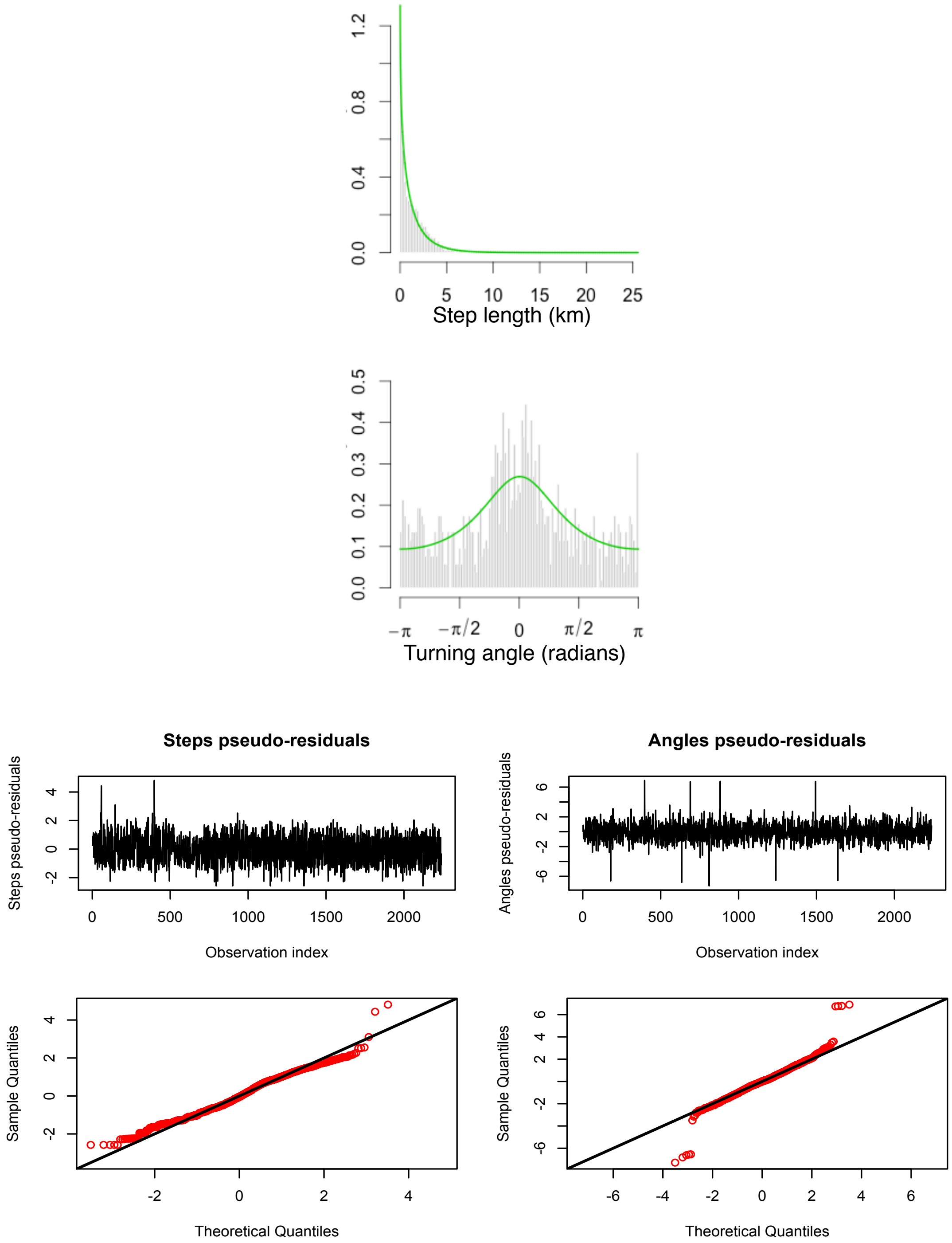

Figure S6.2. Step length and turning angle distributions (top plots) associated with the single-state movement of wolves, as estimated from a hidden Markov model implemented in the R package moveHMM. Bottom plots show pseudo-residuals and normality diagnostic graphs.

REFERENCES

Altendorf, K. B., J. W. Laundré, C. A. L. González, and J. S. Brown (2001). Assessing effects of predation risk on foraging behavior of mule deer. *Journal of Mammalogy* **82**, 430–439.

Basille, M., D. Fortin, C. Dussault, G. Bastille-Rousseau, J. P. Ouellet, and R. Courtois (2015). Plastic response of fearful prey to the spatiotemporal dynamics of predator distribution. *Ecology* **96**, 2622–2631.

Benhamou, S., M. Valeix, S. Chamaillé-Jammes, D. W. Macdonald, and A. J. Loveridge (2014). Movement-based analysis of interactions in African lions. *Animal Behaviour* **90**, 171–180.

Bischof, R., H. Ali, M. Kabir, S. Hameed, and M. A. Nawaz (2014). Being the underdog: an elusive small carnivore uses space with prey and time without enemies. *Journal of Zoology* **293**, 40–48.

Calenge, C. (2006). The package “adehabitat” for the R software: a tool for the analysis of space and habitat use by animals. *Ecological Modelling* **197**, 516–519.

Caro, T. (2005). *Antipredator defenses in birds and mammals*. University of Chicago Press, Chicago.

Cooper Jr, W. E., and D. T. Blumstein (2015). *Escaping from predators: an integrative view of escape decisions*. Cambridge University Press, Cambridge.

Courbin, N., A. J. Loveridge, D. W. Macdonald, H. Fritz, M. Valeix, E. T. Makuwe, and S. Chamaillé-Jammes (2015). Reactive responses of zebras to lion encounters shape their predator–prey space game at large scale. *Oikos*, DOI: 10.1111/oik.02555.

Creel, S., J. Winnie Jr, B. Maxwell, K. Hamlin, and M. Creel (2005). Elk alter habitat selection as an antipredator response to wolves. *Ecology* **86**, 3387–3397.

Creel, S., J. A. Winnie, D. Christianson, and S. Liley (2008). Time and space in general models of antipredator response: tests with wolves and elk. *Animal Behaviour* **76**, 1139–1146.

Cusack, J. J., A. J. Dickman, J. M. Rowcliffe, C. Carbone, D. W. Macdonald, and T. Coulson (2015). Random versus game trail-based camera trap placement strategy for monitoring terrestrial mammal communities. *PLoS One* **10**, e0126373.

Cusack, J. J., A. J. Dickman, M. Kalyahe, J. M. Rowcliffe, C. Carbone, D. W. Macdonald, and T. Coulson (in review). Revealing kleptoparasitic and predatory tendencies in an African mammal community using camera traps: a comparison of spatiotemporal approaches. *Oikos.*

DeAngelis, D. L., K. A. Rose, and M. A. Huston (1994). Individual-oriented approaches to modeling ecological populations and communities. In *Frontiers in Mathematical Biology*, pp. 390-410. Springer Berlin Heidelberg.

Dufrêne, M., and P. Legendre (1997). Species assemblages and indicator species: the need for a flexible asymmetrical approach. *Ecological Monographs* **67**, 345–366.

Gotelli, N. J., and G. R. Graves (1996). *Null models in ecology*. Smithsonian Institution Press, Washington D. C.

Grimm, V. (1999). Ten years of individual-based modelling in ecology: what have we learned and what could we learn in the future? *Ecological Modelling* **115**, 129–148.

Grimm, V., U. Berger, F. Bastiansen, S. Eliassen, V. Ginot, J. Giske, J. Goss-Custard, T. Grand, S. K. Heinz, G. Huse, and A. Huth (2006). A standard protocol for describing individual-based and agent-based models. *Ecological Modelling* **198**, 115–126.

Harmsen, B. J., R. J. Foster, S. C. Silver, L. E. Ostro, and C. P. Doncaster (2011). Jaguar and puma activity patterns in relation to their main prey. *Mammalian Biology-Zeitschrift für Säugetierkunde* **76**, 320–324.

Hernández, L., J. W. Laundré, and M. Gurung (2005). Use of camera traps to measure predation risk in a puma-mule deer system. *Wildlife Society Bulletin* **33**, 353–358.

Kauffman, M. J., N. Varley, D. W. Smith, D. R. Stahler, D. R. MacNulty, and M. S. Boyce (2007). Landscape heterogeneity shapes predation in a newly restored predator–prey system. *Ecology Letters* **10**, 690–700.

Kays, R., B. Kranstauber, P. Jansen, C. Carbone, M. Rowcliffe, T. Fountain, and S. Tilak (2009). Camera traps as sensor networks for monitoring animal communities. *Local Computer Networks, IEEE 34th Conference*, pp. 811–818.

Kays, R., R. Costello, T. Forrester, M. C. Baker, A. W. Parsons, E. L. Kalies, G.

Hess, J. J. Millspaugh, and W. McShea (2015). Cats are rare where coyotes roam. *Journal of Mammalogy* **96**, 981–987.

Langrock, R., R. King, J. Matthiopoulos, L. Thomas, D. Fortin, and J. M. Morales (2012). Flexible and practical modeling of animal telemetry data: hidden Markov models and extensions. *Ecology* **93**, 2336–2342.

Laundré, J. W., L. Hernández, and K. B. Altendorf (2001). Wolves, elk, and bison: reestablishing the" landscape of fear" in Yellowstone National Park, USA. *Canadian Journal of Zoology* **79**, 1401–1409.

Laundré, J. W. (2010). Behavioral response races, predator-prey shell games, ecology of fear, and patch use of pumas and their ungulate prey. *Ecology* **91**, 2995–3007.

Lazenby, B. T., and C. R. Dickman (2013). Patterns of detection and capture are associated with cohabiting predators and prey. *PLoS One* **8**, e59846.

Le Saout, S., J. L. Martin, P. Blanchard, N. Cebe, A. J. Mark Hewison, J. L. Rames, and S. Chamaillé-Jammes (2015). Seeing a ghost? Vigilance and its drivers in a predator-free world. *Ethology* **121**, 651–660.

Lima, S. L., and P. A. Bednekoff (1999). Temporal variation in danger drives antipredator behavior: the predation risk allocation hypothesis. *The American Naturalist* **153**, 649–659.

MacKenzie, D. I., L. L.Bailey, and J. Nichols (2004). Investigating species co-occurrence patterns when species are detected imperfectly. *Journal of Animal Ecology* **73**, 546–555.

Mech, L. D., and L. Boitani (2010). *Wolves: behavior, ecology, and conservation*.

University of Chicago Press, Chicago.

Michelot, T., R. Langrock, and T. A. Patterson (2016). moveHMM: An R package for the statistical modelling of animal movement data using hidden Markov models. *Methods in Ecology and Evolution,* DOI: 10.1111/2041-210X.12578.

Middleton, A. D., M. J. Kauffman, D. E. McWhirter, J. G. Cook, R. C. Cook, A. A. Nelson, M. D. Jimenez, and R. W. Klaver (2013). Animal migration amid shifting patterns of phenology and predation: lessons from a Yellowstone elk herd. *Ecology* **94**, 1245–1256.

Morales, J. M., D. T. Haydon, J. Frair, K. E. Holsinger, and J. M. Fryxell (2004). Extracting more out of relocation data: building movement models as mixtures of random walks. *Ecology* **85**, 2436–2445.

Muhly, T. B., C. Semeniuk, A. Massolo, L. Hickman, and M. Musiani (2011). Human activity helps prey win the predator-prey space race. *PLoS One* **6**, e17050.

O'Connell, A. F., J. D. Nichols, and K. U. Karanth (2010). *Camera traps in animal ecology: methods and analyses*. Springer, Tokyo.

Proffitt, K. M., J. L. Grigg, K. L. Hamlin, and R. A. Garrott (2009). Contrasting effects of wolves and human hunters on elk behavioral responses to predation risk. *The Journal of Wildlife Management* **73**, 345–356.

Pettorelli, N., A. Hilborn, C. Duncan, and S. M. Durant (2015). Chapter Two-Individual variability: the missing component to our understanding of predator–prey interactions. *Advances in Ecological Research* **52**, 19–44.

R Development Core Team (2015). R: a language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. www.rproject.org

Rogala, J. K., M. Hebblewhite, J. Whittington, C. A. White, J. Coleshill, and M. Musiani (2011). Human activity differentially redistributes large mammals in the Canadian Rockies National Parks. *Ecology and Society*, DOI: 10.5751/ES-04251-160316.

Ross, J., A. J. Hearn, P. J. Johnson, and D. W. Macdonald (2013). Activity patterns and temporal avoidance by prey in response to Sunda clouded leopard predation risk. *Journal of Zoology* **290**, 96–106.

Rovero, F., F. Zimmermann, D. Berzi, and P. Meek (2013). " Which camera trap type and how many do I need?" A review of camera features and study designs for a range of wildlife research applications. *Hystrix, the Italian Journal of Mammalogy* **24**, 148–156.

Searle, K. R., C. J. Stokes, and I. J. Gordon (2008). When foraging and fear meet: using foraging hierarchies to inform assessments of landscapes of fear. *Behavioral Ecology* **19**, 475–482.

Sih, A. (1984). The behavioural response race between predator and prey. *The American Naturalist* **123**, 143–150.

Sih, A. (1998). Game theory and predator–prey response races. In *Game theory and animal behaviour*, pp. 221–238. Oxford University Press, Oxford.

Smith, D. W., T. D. Drummer, K. M. Murphy, D. S. Guernsey, and S. B. Evans (2004). Winter prey selection and estimation of wolf kill rates in

Yellowstone National Park, 1995-2000. *The Journal of Wildlife Management* **68**, 153–166.

Sollmann, R., M. M. Furtado, H. Hofer, A. T. Jácomo, N. M. Tôrres, and L. Silveira (2012). Using occupancy models to investigate space partitioning between two sympatric large predators, the jaguar and puma in central Brazil. *Mammalian Biology-Zeitschrift für Säugetierkunde* **77**, 41–46.

Swanson, A., M. Kosmala, C. Lintott, R. Simpson, A. Smith, and C. Packer (2015). Snapshot Serengeti, high-frequency annotated camera trap images of 40 mammalian species in an African savanna. *Scientific Data*, DOI: 10.1038/sdata.2015.26.

Tambling, C. J., L. Minnie, J. Meyer, E. W. Freeman, R. M. Santymire, J. Adendorff, and G. I. Kerley (2015). Temporal shifts in activity of prey following large predator reintroductions. *Behavioral Ecology and Sociobiology* **69**, 1153–1161.

Thaker, M., A. T. Vanak, C. R. Owen, M. B. Ogden, S. M. Niemann, and R. Slotow (2011). Minimizing predation risk in a landscape of multiple predators: effects on the spatial distribution of African ungulates. *Ecology* **92**, 398–407.

Weissburg, M., D. L. Smee, and M. C. Ferner (2014). The sensory ecology of nonconsumptive predator effects. *The American Naturalist* **184**, 141–57.

Zucchini, W., and I. L. MacDonald (2009). *Hidden Markov models for time series: an introduction using R*. Chapman and Hall/CRC Press, London.

Chapter 7

Discussion

Camera trapping is a remarkably powerful and versatile tool with which to study wild animals. As illustrated in this thesis, camera traps have the potential to help answer questions relating to the number of species present in an area (Chapter 2), their relative rarity or commonness (Chapters 2 and 3), and how they might interact (Chapter 4). These are all vital to our understanding of the natural world, but also to the development of effective conservation actions in increasingly threatened environments worldwide. Like all methodologies for surveying wildlife, camera trapping has its limitations and biases, and in this regard it is often useful to contrast its use to that of other common methods of collecting ecological data (Chapter 5). Lastly, ecologists and conservationists have much to gain from simulation exercises that test camera trap study design and feasibility (Chapter 6), particularly since the deployment of camera traps in the field can be costly.

The work in this thesis can be regarded as a gradation in the level of complexity of the attempted inferences, from basic species inventories to intricate interactive behaviour. In all cases, however, the importance of interpreting observed patterns with due regard to both underlying methodological and ecological processes is put forward (Burton et al. 2015). In this discussion, I briefly evaluate the overall implications of my work for future camera trap studies, placing particular emphasis on placement strategy, spatiotemporal patterns, and whether or not camera traps are all we need to study mammal communities. As is often the way in science, I have thrown up as many questions as I have answered, and so offer some thoughts on potential avenues for future research throughout.

Is camera trap placement strategy important?

In savannah ecosystems, choice of placement strategy has the potential to affect the cost-effectiveness of species inventories, rather than the richness or composition of the mammal community ultimately described. This is because, although a species may show a preference for particular features of the landscape (e.g. game trails), use of the latter is very rarely exclusive. In Chapter 2 I found that placing cameras exclusively on game trails in Ruaha's savannah habitat resulted in more species being described as present more quickly, and facilitated the detection of rare species during the wet season relative to a random control. The latter finding is particularly interesting as it suggests that denser vegetation, such as undergrowth in forested environments, may exacerbate differences between trail and random surveys. Few studies have examined the influence of camera trap placement strategy on community-wide patterns in tropical forests (Blake and Mosquera 2014, Di Bitetti et al. 2014), and I call for more experimental studies such as the one described in Chapter 2 to be carried out in these habitats.

When it comes to estimating species density, however, camera trap placement strategy is clearly very important. The application of capture-recapture models to estimate the density of marked species relies heavily on maximising photographic rates (Karanth 1995, Karanth and Nichols 1998, O'Connell et al. 2010, Sollmann et al. 2011), which in the case of carnivores generally implies targeted camera placement (Brassine and Parker 2015), for example on game trails (Silver et al. 2004). This is at odds with the sampling requirement of the REM, which assumes cameras are placed randomly with reference to animal movement (Rowcliffe et al. 2008, 2013). Indeed, Chapter 3 of this thesis showed that the placement of camera traps on isolated savannah trees (a form of non-random placement) led to biased density estimates for female lions. Had the REM been applied to data collected from the random and trail-based surveys implemented in Chapter 2, density estimates for carnivore species in particular would have differed substantially given the notable differences in capture rates between the two survey types. Conversely, spatially explicit capture recapture models applied to leopards (*Panthera pardus*) in Ruaha resulted in more accurate and precise estimates of density when based on photographic data collected using the trail-based placement (Olivieri 2015).

Whereas most carnivores tend to be photographed more often on trails than off them (Negroes et al. 2010, Srbek-Araujo and Chiarello 2013, Mann et al. 2015, Wearn et al. 2013), other trophic groups do not seem to show such a consistent bias (Cusack et al. 2015, Harmsen et al. 2010). This offers some hope that REM methods may be applied to quantify prey densities from camera trap grids designed for the purpose of capture-recapture analyses of medium to large carnivores, thus enabling predator-prey dynamics to be studied in more detail (e.g. Karanth et al. 2004). Such a study has yet to be carried out though, and would represent a very useful addition to the camera trapping literature. Until this is done, a more prudent approach might be to implement a mixed placement strategy, where a proportion of available camera traps are placed randomly (Mann et al. 2015). This approach would be particularly recommended when camera trapping in previously un-surveyed areas, or to ensure a more representative sample of local mammal diversity when conducting rapid biodiversity assessments. In most cases, the implementation of mixed placement strategies will represent a compromise between reducing potential bias in species detection probability and gaining enough power to characterise patterns reliably from either random or non-random subsets.

Although an appropriate sampling design is key to minimising bias in community-level inferences, post-hoc methods for quantifying species richness whilst taking into account imperfect detection are gaining in popularity (Rovero et al. 2014, Tobler et al. 2015, Rich et al. 2016). These methods are often combined with analyses relating to the distribution (or occupancy) of multiple species across a given landscape, thereby enabling inferences to be made about the spatial structure of mammal communities. An exciting prospect for future research will be to link species interactions to patterns of community richness and structure using such models.

Do interactions result in measureable spatiotemporal patterns?

The answer to this question depends largely on the behaviour of each (potentially) interacting species. Two species seeking to avoid each other, such as two sympatric carnivores of similar morphology and ecology (e.g. Vieira and Port 2007), can be expected to segregate their activity in space and/or time so as to avoid harmful encounters or competition (Schoener 1974, Carothers and Jaksic 1984, Schuette et al. 2013, Edwards et al. 2015). Even then, spatiotemporal avoidance patterns may be dampened by differences in diet (Ramesh et al. 2012). On the other hand, the interactions considered in the present thesis (Chapters 4, 5 and 6) are arguably more complex, if only because they involve attraction by the predator/parasite as well as avoidance by the prey/victim. Indeed, theory suggests that the outcome of the spatial race between two species may be perceived as random if both are mobile and respond to one another's presence in opposing ways (Sih 1984). In addition, other mechanisms may enable prey species to remain in close proximity to predators. In the case of elk, this may mean foraging in denser vegetation patches and in larger groups, for example (White et al. 2012).

When spatiotemporal patterns do emerge from interactions, can these be reliably characterised from camera trap data? According to the work carried out in this thesis, not easily. Chapter 6 showed that a huge amount of camera trapping effort would be necessary in order to characterise simulated prey responses to predators. Although the dynamic approaches put forward in Chapter 4 show some promise, ensuring that the temporal scale over which interactive processes are measured matches that of the actual behaviours remains a challenge. As an example, given the strong spatial aggregation of species around the Ruaha River during the dry season, attraction and avoidance patterns are likely to occur over a period of time that is far shorter than the 24 hours considered. Treating time continuously thus appears to be necessary, and is an analytical development I am very keen to pursue in the future.

Finally, while most researchers would agree that the more camera traps the better, giving some thought to study design may enable meaningful patterns to be detected despite limited resources. As hinted at in Chapter 6, comparison of spatiotemporal behaviour between areas with and without a predator or competitor (Ross et al. 2013), or before and after a reintroduction (Tambling et al. 2015), may be more informative so long as spatial and temporal confounding factors are accounted for, respectively. Alternatively, investigating species succession at carcass sites has provided insight into spatiotemporal partitioning in scavenging behaviour between dominant and subordinate carnivores (Forsyth et al. 2014).

Are camera traps all we need?

While the answer to this question is most certainly no, the staggering range of questions that are now being addressed using camera traps is pause for thought. With the exception of species inventories, most of the more advanced assumptions and interpretations presented in this thesis relied on additional information relating to animal behaviour. Application of the REM involved defining what constituted a random camera placement relative to the movement of female lions; spatiotemporal associations between interacting species relied on establishing a prior for the direction of the interaction; and investigating elk responses to wolves benefitted from 20 years of detailed behavioural studies. With this in mind, it is interesting to think of what inferences would have been made without access to additional information. Lion density in the Serengeti would have been severely over-estimated, interactive relationships in Ruaha would have remained unclear, and elk in Yellowstone might have been perceived to behave randomly towards wolves.

Recent years have seen a notable push to extract more information from camera trap images with the aim of enhancing existing approaches. For instance, Rowcliffe et al. (2016) have recently put forward a method to estimate the average speed of a species from sequences of images obtained when individuals pass in front of camera traps. A measure of day range can be obtained by multiplying travel speed by activity level, with the latter also derived from the camera trap data (Rowcliffe et al. 2014). Aside from camera placement, the estimation of average speed of lion movement was a key limitation in Chapter 3, and to the application of the REM in general (Foster and Harmsen 2012, Rovero et al. 2013). These new methods might enable researchers to estimate REM parameters directly from the camera trap data (see also Rowcliffe et al. 2011).

Despite this, we cannot expect camera trapping to provide all the answers when many of the processes underlying observed patterns in photographic data are still not well understood (Burton et al. 2015). These include species-specific movement patterns, which I have shown to be important in Chapters 2 and 3, but also other ecological processes, such as alternative anti-predator behaviours that may not be easily characterised from spatiotemporal data alone (e.g. vigilance levels, fine scale switches in habitat use, group size), even those obtained from GPS collars. Thus, alternative sources of data, such as direct observation or scat analyses, may be necessary. More generally, camera trapping should form part of a more integrative approach whereby multiple methodologies are used to provide additional information and verify assumptions underlying statistical models aimed at making inferences on the patterns and processes inherent to mammal communities (Gompper et al. 2006, Soisalo and Cavalcanti 2006, Gopalaswamy et al. 2012, Swan et al. 2014).

References

Ahumada, J.A., C. E. Silva, K. Gajapersad, C. Hallam, J. Hurtado, E. Martin, A. McWilliams, B. Mugerwa, T. O'Brien, F. Rovero, D. Sheil, W. R. Spironello, N. Wnarni, and S. Andelman (2011). Community structure and diversity of tropical forest mammals: data from a global camera trap network. *Philosophical Transactions of the Royal Society B: Biological Sciences* **366**, 2703–2711.

Ahumada, J. A., J. Hurtado, and D. Lizcano (2013). Monitoring the status and trends of tropical forest terrestrial vertebrate communities from camera trap data: a tool for conservation. *PLoS One* **8**, e73707.

Alexander, J. S., A. M. Gopalaswamy, K. Shi, and P. Riordan (2015). Face value: towards robust estimates of snow leopard densities. *PLoS One* **10**, e0134815.

Anile, S., and S. Devillard (2015). Study design and body mass influence RAIs from camera trap studies: evidence from the Felidae. *Animal Conservation* **19**, 35–45.

Basille, M., D. Fortin, C. Dussault, G. Bastille-Rousseau, J. P. Ouellet, and R. Courtois (2015). Plastic response of fearful prey to the spatiotemporal dynamics of predator distribution. *Ecology* **96**, 2622–2631.

Benhamou, S., M. Valeix, S. Chamaillé-Jammes, D. W. Macdonald, and A. J. Loveridge (2014). Movement-based analysis of interactions in African lions. *Animal Behaviour* **90**, 171–180.

Bischof, R., H. Ali, M. Kabir, S. Hameed, and M. A. Nawaz (2014). Being the underdog: an elusive small carnivore uses space with prey and time without enemies. *Journal of Zoology* **293**, 40–48.

Blake, J. G., and D. Mosquera (2014). Camera trapping on and off trails in lowland forest of eastern Ecuador: does location matter? *Mastozoología Neotropical* **21**, 17–26.

Borchers, D. L., and M. G. Efford (2008). Spatially explicit maximum likelihood methods for capture–recapture studies. *Biometrics* **64**, 377–385.

Brassine, E., and D. Parker (2015). Trapping Elusive Cats: Using Intensive Camera Trapping to Estimate the Density of a Rare African Felid. *PLoS One* **10**, e0142508.

Broekhuis, F., G. Cozzi, M. Valeix, J. W. McNutt, and D. W. Macdonald (2013). Risk avoidance in sympatric large carnivores: reactive or predictive? *Journal of Animal Ecology* **82**, 1098–1105.

Burton, A. C., E. Neilson, D. Moreira, A. Ladle, R. Steenweg, J. T. Fisher, E. Bayne, and S. Boutin (2015). Wildlife camera trapping: a review and recommendations for linking surveys to ecological processes. *Journal of Applied Ecology* **52**, 675–685.

Carbone, C., S. Christie, K. Conforti, T. Coulson, N. Franklin, J. R. Ginsberg, M. Griffiths, J. Holden, K. Kawanishi, M. Kinnaird, R. Laidlaw, A. Lynam, D. W. Macdonald, D. Martyr, C. MacDougal, L. Nath, T. O'Brien, J. Seidensticker, D. J. L. Smith, M. Sunquist, R. Tilson, and W. N. Shahruddin (2001). The use of photographic rates to estimate densities of tigers and other cryptic mammals. *Animal Conservation* **4**, 75–79.

Caro, T. (2005). *Antipredator defenses in birds and mammals*. University of Chicago Press.

Carothers, J. H., and F. M. Jaksić (1984). Time as a niche difference: the role of interference competition. *Oikos* **42**, 403–406.

Chandler, R. B., and J. A. Royle (2013). Spatially explicit models for inference about density in unmarked or partially marked populations. *The Annals of Applied Statistics* **7**, 936–954.

Colwell, R. K., C. X. Mao, and J. Chang (2004). Interpolating, extrapolating, and comparing incidence-based species accumulation curves. *Ecology* **85**, 2717–2727.

Courbin, N., A. J. Loveridge, D. W. Macdonald, H. Fritz, M. Valeix, E. T. Makuwe, and S. Chamaillé-Jammes (2015). Reactive responses of zebras to lion encounters shape their predator–prey space game at large scale. *Oikos*, DOI: 10.1111/oik.02555.

Creel, S., J. Winnie Jr, B. Maxwell, K. Hamlin, and M. Creel (2005). Elk alter habitat selection as an antipredator response to wolves. *Ecology* **86**, 3387–3397.

Creel, S., J. A. Winnie, D. Christianson, and S. Liley (2008). Time and space in general models of antipredator response: tests with wolves and elk. *Animal Behaviour* **76**, 1139–1146.

Cusack, J. J., A. J. Dickman, J. M. Rowcliffe, C. Carbone, D. W. Macdonald, and T. Coulson (2015). Random versus Game Trail-Based Camera Trap Placement Strategy for Monitoring Terrestrial Mammal Communities. *PLoS One* **10**, e0126373.

Davison, A., J. D. Birks, R. C. Brookes, T. C. Braithwaite, and J. E. Messenger (2002). On the origin of faeces: morphological versus molecular methods for surveying rare carnivores from their scats. *Journal of Zoology* **257**, 141–143.

Di Bitetti, M. S., A. Paviolo, A., and C. De Angelo (2014). Camera trap photographic rates on roads vs. off roads: location does matter. *Mastozoología Neotropical* **21**, 37–46.

Dorazio, R. M., J. A. Royle, B. Söderström, and A. Glimskär (2006). Estimating species richness and accumulation by modeling species occurrence and detectability. *Ecology* **87**, 842–854.

du Preez, B., T. Hart, A. J. Loveridge, and D. W. Macdonald (2015). Impact of risk on animal behaviour and habitat transition probabilities. *Animal Behaviour* **100**, 22–37.

Edwards, S., A. C. Gange, and I. Wiesel (2015). Spatiotemporal resource partitioning of water sources by African carnivores on Namibian commercial farmlands. *Journal of Zoology* **297**, 22–31.

Efford, M. G., D. K. Dawson, and C. S. Robbins (2004). DENSITY: software for analysing capture-recapture data from passive detector arrays. *Animal Biodiversity and Conservation* **27**, 217–228.

Forsyth, D. M., L. Woodford, P. D. Moloney, J. O. Hampton, A. P. Woolnough, and M. Tucker (2014). How does a carnivore guild utilise a substantial but unpredictable anthropogenic food source? Scavenging on hunter-shot ungulate carcasses by wild dogs/dingoes, red foxes and feral cats in South-Eastern Australia revealed by camera traps. *PLoS One* **9**, e97937.

Fortin, D., H. L. Beyer, M. S. Boyce, D. W. Smith, T. Duchesne, and J. S. Mao (2005). Wolves influence elk movements: behavior shapes a trophic cascade in Yellowstone National Park. *Ecology* **86**, 1320–1330.

Foster, R. J., and B. J. Harmsen (2012). A critique of density estimation from camera-trap data. *The Journal of Wildlife Management* **76**, 224–236.

Gompper, M. E., R. W. Kays, J. C. Ray, S. D. Lapoint, D. A. Bogan, and J. R. Cryan (2006). A comparison of noninvasive techniques to survey carnivore communities in northeastern North America. *Wildlife Society Bulletin* **34**, 1142–1151.

Gompper, M. E., D. B. Lesmeister, J. C. Ray, J. R. Malcolm, and R. Kays (2016). Differential Habitat Use or Intraguild Interactions: What Structures a Carnivore Community? *PLoS One* **11**, e0146055.

Gopalaswamy, A. M., J. A. Royle, M. Delampady, J. D. Nichols, K. U. Karanth, and D. W. Macdonald (2012). Density estimation in tiger populations: combining information for strong inference. *Ecology* **93**, 1741–1751.

Gotelli, N. J., and G. R. Graves (1996). *Null Models in Ecology*. Smithsonian Institution Press, Washington D. C.

Grant, P. R. (1972). Interspecific competition among rodents. *Annual Review of Ecology and Systematics* **3**, 79–106.

Harmsen, B. J., R. J. Foster, S. Silver, L. Ostro, and C. P. Doncaster (2010). Differential Use of Trails by Forest Mammals and the Implications for Camera-Trap Studies: A Case Study from Belize. *Biotropica* **42**, 126–133.

Hebblewhite, M., and E. Merrill (2008). Modelling wildlife–human relationships for social species with mixed-effects resource selection models. *Journal of Applied Ecology* **45**, 834–844.

Hutchinson, J., and P. M. Waser (2007). Use, misuse and extensions of "ideal gas" models of animal encounter. *Biological Reviews* **82**, 335–359.

Ikeda, T., H. Takahashi, T. Yoshida, H. Igota, Y. Matsuura, K. Takeshita, and K. Kaji (2015). Seasonal Variation of Activity Pattern in Sika Deer (*Cervus nippon*) as Assessed by Camera Trap Survey. *Mammal Study* **40**, 199–205.

Jenks, K. E., P. Chanteap, K. Damrongchainarong, P. Cutter, P. Cutter, T. Redford, A. J. Lynam, J. Howard, and P. Leimgruber (2011). Using relative abundance indices from camera-trapping to test wildlife conservation hypotheses-an example from Khao Yai National Park, Thailand. *Tropical Conservation Science* **4**, 113–131.

Jennelle, C. S., M. C. Runge, and D. I. MacKenzie (2002). The use of photographic rates to estimate densities of tigers and other cryptic mammals: a comment on misleading conclusions. *Animal Conservation* **5**, 119–120.

Karanth, K. U. (1995). Estimating tiger *Panthera tigris* populations from camera-trap data using capture—recapture models. *Biological Conservation* **71**, 333–338.

Karanth, K. U., and J. D. Nichols (1998). Estimation of tiger densities in India using photographic captures and recaptures. *Ecology* **79**, 2852–2862.

Karanth, K. U., J. D. Nichols, N. S. Kumar, W. A. Link, and J. E. Hines (2004). Tigers and their prey: predicting carnivore densities from prey abundance. *Proceedings of the National Academy of Sciences of the United States of America* **101**, 4854–4858.

Kauffman, M. J., M. Sanjayan, J. Lowenstein, A. Nelson, R. M. Jeo, and K. R. Crooks (2007a). Remote camera-trap methods and analyses reveal impacts of rangeland management on Namibian carnivore communities. *Oryx* **41**, 70–78.

Kauffman, M. J., N. Varley, D. W. Smith, D. R. Stahler, D. R. MacNulty, and M. S. Boyce (2007b). Landscape heterogeneity shapes predation in a newly restored predator–prey system. *Ecology Letters* **10**, 690–700.

Kauffman, M. J., J. F. Brodie, and E. S. Jules (2010). Are wolves saving Yellowstone's aspen? A landscape-level test of a behaviorally mediated trophic cascade. *Ecology* **91**, 2742–2755.

Kays, R., R. Costello, T. Forrester, M. C. Baker, A. W. Parsons, E. L. Kalies, G. Hess, J. J. Millspaugh, and W. McShea (2015a). Cats are rare where coyotes roam. *Journal of Mammalogy* **96**, 981–987.

Kays, R., M. C. Crofoot, W. Jetz, and M. Wikelski (2015b). Terrestrial animal tracking as an eye on life and planet. *Science* **348**, aaa2478.

Kelly, M. J., and E. L. Holub (2008). Camera trapping of carnivores: trap success among camera types and across species, and habitat selection by species, on Salt Pond Mountain, Giles County, Virginia. *Northeastern Naturalist* **15**, 249–262.

Kelly, M. J., A. J. Noss, M. S. Di Bitetti, L. Maffei, R. L. Arispe, A. Paviolo, C. D. De Angelo, and Y. E. Di Blanco (2008). Estimating puma densities from camera trapping across three study sites: Bolivia, Argentina, and Belize. *Journal of Mammalogy* **89**, 408–418.

Kinnaird, M. F., and T. G. O'Brien (2012). Effects of Private-Land Use, Livestock Management, and Human Tolerance on Diversity, Distribution, and Abundance of Large African Mammals. *Conservation Biology* **26**, 1026–1039.

Klare, U., J. F. Kamler, and D. W. Macdonald (2011). A comparison and critique of different scat-analysis methods for determining carnivore diet. *Mammal Review* **41**, 294–312.

Laundré, J. W., L. Hernández, K. B. Altendorf (2001). Wolves, elk, and bison: reestablishing the" landscape of fear" in Yellowstone National Park, USA. *Canadian Journal of Zoology* **79**, 1401–1409.

Laundré, J. W., L. Hernández, and W. J. Ripple (2010). The landscape of fear: ecological implications of being afraid. *Open Ecology Journal* **3**, 1–7.

Lendrum, P. E., C. R. Anderson Jr, K. L. Monteith, J. A. Jenks, and R. T. Bowyer (2013). Migrating mule deer: effects of anthropogenically altered landscapes. *PLoS One* **8**, e64548.

Lesmeister, D. B., C. K. Nielsen, E. M. Schauber, and E. C. Hellgren (2015). Spatial and temporal structure of a mesocarnivore guild in midwestern north America. *Wildlife Monographs* **191**, 1–61.

Linkie, M., and M. S. Ridout (2011). Assessing tiger–prey interactions in Sumatran rainforests. *Journal of Zoology* **284**, 224–229.

Long, R. A., P. MacKay, J. Ray, and W. Zielinski (2012). *Noninvasive Survey Methods for Carnivores*. Island Press, Washington D.C.

Long, J. A., T. A. Nelson, S. L. Webb, and K. L. Gee (2014). A critical examination of indices of dynamic interaction for wildlife telemetry studies. *Journal of Animal Ecology* **83**, 1216–1233.

MacKenzie, D. I., J. D. Nichols, G. B. Lachman, S. Droege, J. A. Royle, and C. A. Langtimm (2002). Estimating site occupancy rates when detection probabilities are less than one. *Ecology* **83**, 2248–2255.

MacKenzie, D. I., L. L. Bailey, and J. Nichols (2004). Investigating species co-occurrence patterns when species are detected imperfectly. *Journal of Animal Ecology* **73**, 546–555.

Mann, G. K., M. J. O'Riain, and D. M. Parker (2015). The road less travelled:

assessing variation in mammal detection probabilities with camera traps in a semi-arid biodiversity hotspot. *Biodiversity and Conservation* **24**, 531–545.

McCallum, J. (2013). Changing use of camera traps in mammalian field research: habitats, taxa and study types. *Mammal Review* **43**, 196–206.

Mech, L. D. (1970). *The Wolf: The Ecology and Behavior of an Endangered Species*. Natural History Press, New York.

Meek, P. D., G. Ballard, and P. Fleming (2012). *An introduction to camera trapping for wildlife surveys in Australia.* Invasive Animals CRC, Canberra.

Meek, P. D., P. J. S. Fleming, A. G. Ballard, P. B. Banks, A. W. Claridge, J. G. Sanderson, and D. E. Swann (2014a). *Camera trapping: wildlife management and research.* CSIRO Publishing, Melbourne, Australia.

Meek, P. D., G. Ballard, A. Claridge, R. Kays, K. Moseby, T. O'Brien, A. O'Connell, J. Sanderson, D. E. Swann, M. Tobler, and S. Townsend (2014b). Recommended guiding principles for reporting on camera trapping research. *Biodiversity and Conservation* **23**, 2321–2343.

Merrill, E., H. Sand, B. Zimmermann, H. McPhee, N. Webb, M. Hebblewhite, P. Wabakken, and J. L. Frair (2010). Building a mechanistic understanding of predation with GPS-based movement data. *Philosophical Transactions of the Royal Society of London B: Biological Sciences* **365**, 2279–2288.

Middleton, A. D., M. J. Kauffman, D. E. McWhirter, M. D. Jimenez, R. C.

Cook, J. G. Cook, S. H. Albeke, H. Sawyer, and P. J. White (2013). Linking anti-predator behaviour to prey demography reveals limited risk effects of an actively hunting large carnivore. *Ecology Letters* **16**, 1023–1030.

Negrões, N., P. Sarmento, J. Cruz, C. Eira, E. Revilla, C. Fonseca, R. Sollmann, N. M. Tôrres, M. M. Furtado, A. T. A. Jácomo, and L. Silveira (2010). Use of camera-trapping to estimate puma density and influencing factors in central Brazil. *The Journal of Wildlife Management* **74**, 1195–1203.

O'Connell, A. F., J. D. Nichols, and K. U. Karanth (2010). *Camera traps in animal ecology: methods and analyses*. Springer Science & Business Media, Tokyo.

Oliveira-Santos, L. G. R., M. A. Tortato, and M. E. Graipel (2008). Activity pattern of Atlantic Forest small arboreal mammals as revealed by camera traps. *Journal of Tropical Ecology* **24**, 563–567.

Olivieri, A. (2015). *Comparing camera trapping to citizen science to produce leopard* Panthera pardus *population science estimates: a case study from Ruaha National Park, Tanzania* MSc Thesis. Imperial College London, UK.

Oriol-Cotterill, A., M. Valeix, L. G. Frank, C. Riginos, and D. W. Macdonald (2015). Landscapes of Coexistence for terrestrial carnivores: the ecological consequences of being downgraded from ultimate to penultimate predator by humans. *Oikos* **124**, 1263–1273.

Painter, L. E., R. L. Beschta, E. J. Larsen, and W. J. Ripple (2015). Recovering aspen follow changing elk dynamics in Yellowstone: evidence of a trophic cascade? *Ecology* **96**, 252–263.

Piggott, M. P., and A. C. Taylor (2003). Remote collection of animal DNA and its applications in conservation management and understanding the population biology of rare and cryptic species. *Wildlife Research* **30**, 1–13.

Pimm, S. L., S. Alibhai, R. Bergl, A. Dehgan, C. Giri, Z. Jewell, L. Joppa, R. Kays, and S. Loarie (2015). Emerging technologies to conserve biodiversity. *Trends in Ecology and Evolution* **30**, 685–696.

Potts, J. R., K. Mokross, and M. A. Lewis (2014). A unifying framework for quantifying the nature of animal interactions. *Journal of The Royal Society Interface* **11**, 20140333.

Proffitt, K. M., J. L. Grigg, K. L. Hamlin, and R. A. Garrott (2009). Contrasting effects of wolves and human hunters on elk behavioral responses to predation risk. *The Journal of Wildlife Management* **73**, 345–356.

Qi, J., Q. Shi, G. Wang, Z. Li, Q. Sun, Y. Hua, and G. Jiang (2015). Spatial distribution drivers of Amur leopard density in northeast China. *Biological Conservation* **191**, 258–265.

Ramesh, T., R. Kalle, K. Sankar, and Q. Qureshi (2012). Spatio-temporal partitioning among large carnivores in relation to major prey species in Western Ghats. *Journal of Zoology* **287**, 269–275.

Rich, L. N., D. A. Miller, H. S. Robinson, J. W. McNutt, and M. J. Kelly (2016). Using camera trapping and hierarchical occupancy modelling to evaluate the spatial ecology of an African mammal community. *Journal of Applied Ecology*, DOI: 10.1111/1365-2664.12650.

Richard, E., C. Calenge, S. Saïd, J. L. Hamann, and J. M. Gaillard (2013). Studying spatial interactions between sympatric populations of large herbivores: a null model approach. *Ecography* **36**, 157–165.

Ridout, M. S., and M. Linkie (2009). Estimating overlap of daily activity patterns from camera trap data. *Journal of Agricultural, Biological, and Environmental Statistics* **14**, 322–337.

Ripple, W. J., E. J. Larsen, R. A. Renkin, and D. W. Smith (2001). Trophic cascades among wolves, elk and aspen on Yellowstone National Park's northern range. *Biological Conservation* **102**, 227–234.

Ripple, W. J., and R. L. Beschta (2012). Trophic cascades in Yellowstone: The first 15years after wolf reintroduction. *Biological Conservation* **145**, 205–213.

Rogala, J. K., M. Hebblewhite, J. Whittington, C. A. White, J. Coleshill, and M. Musiani (2011). Human activity differentially redistributes large mammals in the Canadian Rockies National Parks. *Ecology and Society*, DOI: 10.5751/ES-04251-160316.

Ross, J., A. J. Hearn, P. J. Johnson, and D. W. Macdonald (2013). Activity patterns and temporal avoidance by prey in response to Sunda clouded leopard predation risk. *Journal of Zoology* **290**, 96–106.

Rovero, F., G. B. Rathbun, A. Perkin, T. Jones, D. O. Ribble, C. Leonard, R. R. Mwakisoma, and N. Doggart (2008). A new species of giant sengi or elephant-shrew (genus *Rhynchocyon*) highlights the exceptional biodiversity of the Udzungwa Mountains of Tanzania. *Journal of Zoology* **274**, 126–133.

Rovero, F., F. Zimmermann, D. Berzi, and P. Meek (2013). " Which camera trap type and how many do I need?" A review of camera features and study designs for a range of wildlife research applications. *Hystrix, the Italian Journal of Mammalogy* **24**, 148–156.

Rovero, F., E. Martin, M. Rosa, J. A. Ahumada, and D. Spitale (2014). Estimating species richness and modelling habitat preferences of tropical forest mammals from camera trap data. *PLoS One* **9**, e103300.

Rowcliffe, J. M., and C. Carbone (2008). Surveys using camera traps: are we looking to a brighter future? *Animal Conservation* **11**, 185–186.

Rowcliffe, J. M., J. Field, S. T. Turvey, and C. Carbone (2008). Estimating animal density using camera traps without the need for individual recognition. *Journal of Applied Ecology* **45**, 1228–1236.

Rowcliffe, J. M., C. Carbone, P. A. Jansen, R. Kays, and B. Kranstauber (2011). Quantifying the sensitivity of camera traps: an adapted distance sampling approach. *Methods in Ecology and Evolution* **2**, 464–476.

Rowcliffe, J. M., R. Kays, C. Carbone, and P. A. Jansen (2013). Clarifying assumptions behind the estimation of animal density from camera trap rates. *The Journal of Wildlife Management* **77**, 876–876.

Rowcliffe, J. M., R. Kays, B. Kranstauber, C. Carbone, and P. A. Jansen (2014). Quantifying levels of animal activity using camera trap data. *Methods* *in Ecology and Evolution* **5**, 1170–1179.

Rowcliffe, J. M., P. A. Jansen, R. Kays, B. Kranstauber, and C. Carbone (2016). Wildlife speed cameras: measuring animal travel speed and day range using camera traps. *Remote Sensing in Ecology and Conservation*, DOI: 10.1002/rse2.17.

Royle, J. A., J. D. Nichols, K. U. Karanth, and A. M. Gopalaswamy (2009). A hierarchical model for estimating density in camera-trap studies. *Journal of Applied Ecology* **46**, 118–127.

Schoener, T. W. (1974). Resource partitioning in ecological communities. *Science* **185**, 27–39.

Schuette, P., A. P. Wagner, M. E. Wagner, and S. Creel (2013). Occupancy patterns and niche partitioning within a diverse carnivore community exposed to anthropogenic pressures. *Biological Conservation* **158**, 301–312.

Sih, A. (1984). The behavioural response race between predator and prey. *The American Naturalist* **123**, 143–150.

Silver, S. C., L. E. Ostro, L. K. Marsh, L. Maffei, A. J. Noss, M. J. Kelly, R. B. Wallace, H. Gómez, and G. Ayala (2004). The use of camera traps for estimating jaguar *Panthera onca* abundance and density using capture/recapture analysis. *Oryx* **38**, 148–154.

Smith, D. W., T. D. Drummer, K. M. Murphy, D. S. Guernsey, and S. B. Evans (2004). Winter prey selection and estimation of wolf kill rates in Yellowstone National Park, 1995-2000. *The Journal of Wildlife*

Management **68**, 153–166.

Soisalo, M. K., and S. M. Cavalcanti (2006). Estimating the density of a jaguar population in the Brazilian Pantanal using camera-traps and capture–recapture sampling in combination with GPS radio-telemetry. *Biological Conservation* **129**, 487–496.

Sollmann, R., M. M. Furtado, B. Gardner, H. Hofer, A. T. Jácomo, N. M. Tôrres, and L. Silveira (2011). Improving density estimates for elusive carnivores: accounting for sex-specific detection and movements using spatial capture–recapture models for jaguars in central Brazil. *Biological Conservation* **144**, 1017–1024.

Sollmann, R., A. Mohamed, H. Samejima, and A. Wilting (2013). Risky business or simple solution–Relative abundance indices from camera-trapping. *Biological Conservation* **159**, 405–412.

Srbek-Araujo, A. C., and A. G. Chiarello (2013). Influence of camera-trap sampling design on mammal species capture rates and community structures in southeastern Brazil. *Biota Neotropica* **13**, 51–62.

Sunarto, S., M. J. Kelly, K. Parakkasi, and M. B. Hutajulu (2015). Cat coexistence in central Sumatra: ecological characteristics, spatial and temporal overlap, and implications for management. *Journal of Zoology* **296**, 104–115.

Swan, M., J. Di Stefano, F. Christie, E. Steel, and A. York (2014). Detecting mammals in heterogeneous landscapes: implications for biodiversity monitoring and management. *Biodiversity and Conservation* **23**, 343–355.

Swanson, A., M. Kosmala, C. Lintott, R. Simpson, A. Smith, and C. Packer (2015). Snapshot Serengeti, high-frequency annotated camera trap images of 40 mammalian species in an African savanna. *Scientific data*, DOI: 10.1038/sdata.2015.26.

Tambling, C. J., L. Minnie, J. Meyer, E. W. Freeman, R. M. Santymire, J. Adendorff, and G. I. Kerley (2015). Temporal shifts in activity of prey following large predator reintroductions. *Behavioral Ecology and Sociobiology* **69**, 1153–1161.

Terborgh, J., L. Lopez, P. Nunez, M. Rao, G. Shahabuddin, G. Orihuela, M. Riveros, R. Ascanio, G. H. Adler, T. D. Lambert, and L. Balbas (2001). Ecological meltdown in predator-free forest fragments. *Science* **294**, 1923–1926.

Thirgood, S., A. Mosser, S. Tham, G. Hopcraft, E. Mwangomo, T. Mlengeya, M. Kilewo, J. Fryxell, A. R. E. Sinclair, and M. Borner (2004). Can parks protect migratory ungulates? The case of the Serengeti wildebeest. *Animal Conservation* **7**, 113–120.

Tobler, M. W., S. E. Carrillo-Percastegui, R. Leite Pitman, R. Mares, and G. Powell (2008a). An evaluation of camera traps for inventorying large- and medium-sized terrestrial rainforest mammals. *Animal Conservation* **11**, 169–178.

Tobler, M. W., S. E. Carrillo-Percastegui, R. Leite Pitman, R., Mares, and G. Powell (2008b). Further notes on the analysis of mammal inventory data collected with camera traps. *Animal Conservation* **11**, 187–189.

Tobler, M. W., A. Zúñiga Hartley, S. E. Carrillo-Percastegui, and G. V. Powell (2015). Spatiotemporal hierarchical modelling of species richness and occupancy using camera trap data. *Journal of Applied Ecology* **52**, 413–421.

Valeix, M., A. J. Loveridge, S. Chamaillé-Jammes, Z. Davidson, F. Murindagomo, H. Fritz, and D. W. Macdonald (2009). Behavioral adjustments of African herbivores to predation risk by lions: spatiotemporal variations influence habitat use. *Ecology* **90**, 23–30.

van Schaik, C. P., and M. Griffiths (1996). Activity periods of Indonesian rain forest mammals. *Biotropica* **28**, 105–112.

Veech, J. A. (2013). A probabilistic model for analysing species co-occurrence. *Global Ecology and Biogeography* **22**, 252–260.

Vieira, E. M., and D. Port (2007). Niche overlap and resource partitioning between two sympatric fox species in southern Brazil. *Journal of Zoology* **272**, 57–63.

Waddle, J. H., R. M. Dorazio, S. C. Walls, K. G. Rice, J. Beauchamp, M. J. Schuman, and F. J. Mazzotti (2010). A new parameterization for estimating co-occurrence of interacting species. *Ecological Applications* **20**, 1467–1475.

Wang, S. W., and D. W. Macdonald (2009). The use of camera traps for estimating tiger and leopard populations in the high altitude mountains of Bhutan. *Biological Conservation* **142**, 606–613.

Wearn, O. R., J. M. Rowcliffe, C. Carbone, H. Bernard, H., and R. M. Ewers

(2013). Assessing the status of wild felids in a highly-disturbed commercial forest reserve in Borneo and the implications for camera trap survey design. *PLoS One* **8**, e77598.

White, P. J., K. M. Proffitt, and T. O. Lemke (2012). Changes in elk distribution and group sizes after wolf restoration. *The American Midland Naturalist* **167**, 174–187.

Appendix

Conservation of snow leopards: spill-over benefits for other carnivores?

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Conservation of snow leopards: spill-over benefits for other carnivores?

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Abstract In high-altitude settings of Central Asia the Endangered snow leopard *Panthera uncia* has been recognized as a potential umbrella species. As a first step in assessing the potential benefits of snow leopard conservation for other carnivores, we sought a better understanding of the presence of other carnivores in areas occupied by snow leopards in China's Qilianshan National Nature Reserve. We used camera-trap and sign surveys to examine whether other carnivores were using the same travel routes as snow leopards at two spatial scales. We also considered temporal interactions between species. Our results confirm that other carnivores, including the red fox *Vulpes vulpes*, grey wolf *Canis lupus*, Eurasian lynx *Lynx lynx* and dhole *Cuon alpinus*, occur along snow leopard travel routes, albeit with low detection rates. Even at the smaller scale of our camera trap survey all five carnivores (snow leopard, lynx, wolf, red fox and dhole) were observed. Kernel density estimates suggested a high degree of temporal overlap between the snow leopard and the fox, and the snow leopard and the lynx, as indicated by high overlap coefficient estimates. There is an opportunity to consider protective measures at the local scale that would benefit various species simultaneously. However, it should also be recognized that snow leopard conservation efforts could exacerbate human–wildlife conflicts through their protective effect on other carnivore species.

Keywords China, conservation, Eurasian lynx, grey wolf, red fox, snow leopard

Introduction

In any given landscape, protecting a priority species may have spill-over benefits for other species (Caro, 2003). So-called umbrella species are characterized as requiring sufficiently large areas of habitat that investment in their protection will also benefit many other species (Noss, 1990; Andelman & Fagan, 2000). Top predators often meet this criterion (Sergio et al., 2006; Dalerum et al., 2008; Rozylowicz et al., 2011), with many large carnivores additionally possessing charismatic qualities and wide public recognition that can attract disproportionate conservation investments (Sergio et al., 2006; Karanth & Chellam, 2009). The flagship status of such carnivores can bring indirect benefits to other species that are neglected or overlooked, by highlighting common threats and emphasizing their mutual dependence. A fundamental step in identifying and quantifying potential benefits for other species is to demonstrate the spatial extent of co-occurrence in the area of interest (Andelman & Fagan, 2000).

In the mountains of Central Asia the Endangered snow leopard *Panthera uncia* (Jackson et al., 2008) has been highlighted as a potential umbrella species (Bhatnagar et al., 2002; Snow Leopard Network, 2014). The snow leopard has acquired an iconic status worldwide and is being promoted as a flagship species (Snow Leopard Working Secretariat, 2013). Snow leopards are known to have large home ranges and their geographical distribution overlaps with that of other carnivores, such as the grey wolf *Canis lupus*, Eurasian lynx *Lynx lynx* and red fox *Vulpes vulpes* (Fig. 1). There have been few quantitative investigations of the interactions of snow leopards with these other carnivore species (Jumabay-Uulu et al., 2014; Li et al., 2013), which all tend to be regarded negatively by local herding communities and are consequently vulnerable to retaliatory killing (Ale et al., 2007; Worthy & Foggin, 2008; Alexander et al., 2015a).

As a first step in assessing the potential impacts of snow leopard conservation on sympatric carnivores, we investigated the presence of other carnivores within snow leopard areas. We combined fine-scale camera trap data with wider landscape-scale data from sign surveys to determine the degree to which other carnivores use the same travel routes as snow leopards. We also examined temporal activity patterns and the consequences for potential interspecific interactions.

Methods

Fieldwork was conducted in Qilianshan National Nature Reserve, in the south-central part of Gansu Province, China. Camera trap data were collected from a total of 72 camera trap stations, each consisting of a single camera

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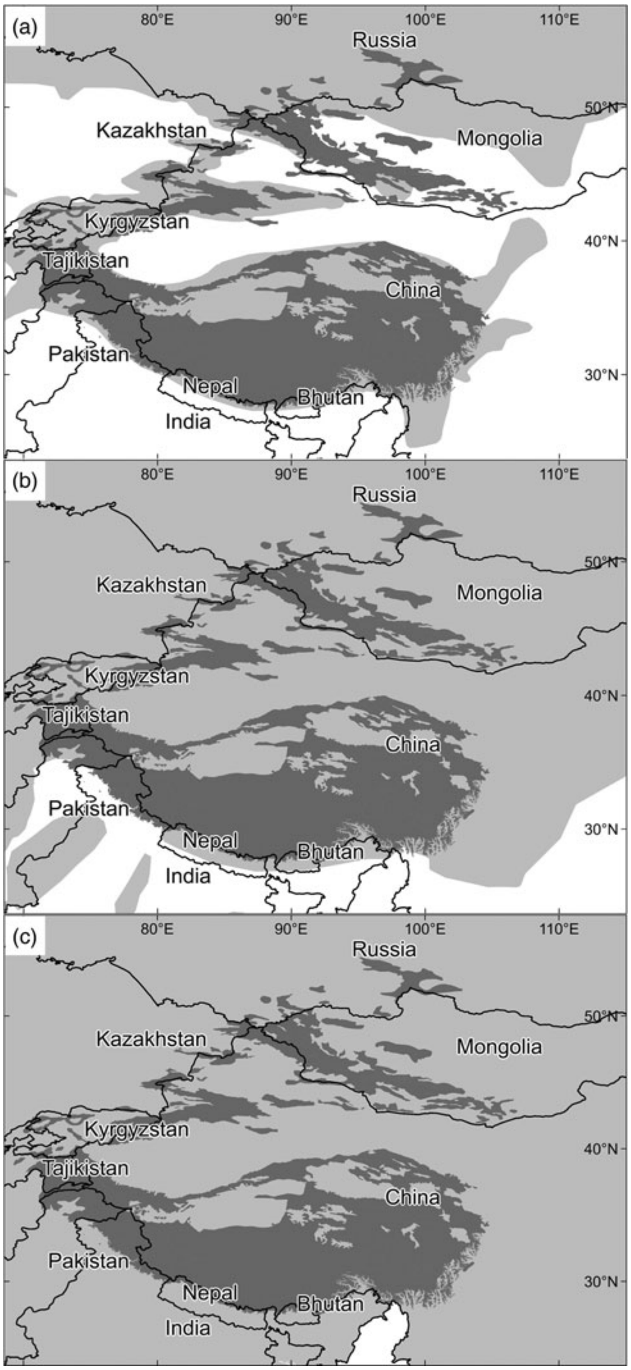

FIG. 1 Distribution of the snow leopard *Panthera uncia* (dark grey shading), the Eurasian lynx *Lynx lynx* (light grey, a), grey wolf *Canis lupus* (light grey, b) and red fox *Vulpes vulpes* (light grey, c). Total overlap in the distribution of snow leopards and that of wolves, lynx and red foxes is 97, 100 and 100%, respectively (IUCN, 2015).

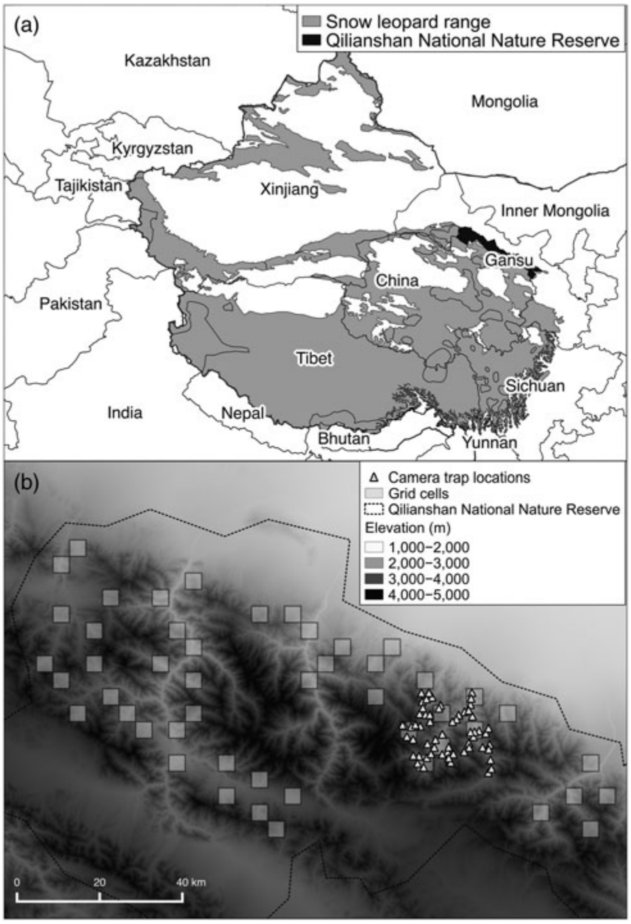

FIG. 2 (a) Location of Qilianshan National Nature Reserve, Gansu Province China. (b) Locations of camera traps and grid cells in which transect surveys were conducted in the Reserve.

trap unit, within a 480 km^2 area (Fig. 2). A pilot study conducted at this site in 2012 had confirmed the presence of snow leopards. Sixty camera trap stations were active during January–March 2013 (Alexander et al., 2015b). During April 2013–July 2014 we maintained 23 of these camera trap stations and added an additional 12 stations to maximize the number of capture events. As our target species was the snow leopard, the locations of camera trap stations were chosen based on the high density of snow leopard signs, and on the presence of natural pathways (such as ridges and valleys) that individual snow leopards were likely to use. We recorded capture histories for each carnivore species, also noting the time of capture. To avoid pseudoreplication, when the same species was captured more than once during a period of < 30 minutes only the first occasion was recorded as an independent capture event.

The times of each independent event were partitioned into hourly intervals to establish 24-hour activity patterns for each species. Temporal interspecific interactions were investigated by estimating the kernel density of temporal overlap (Ridout & Linkie, 2009). We compared the temporal activity patterns of snow leopards with those of the red fox and the Eurasian lynx by estimating the coefficient of overlap (Δ_4 and Δ_1), ranging from 0 (no overlap) to 1 (complete overlap). Confidence intervals at 95% were obtained as percentile intervals from 500 bootstrap samples

TABLE 1 Results of camera trap and transect surveys of carnivores in Qilianshan National Nature Reserve, China, with species, no. of camera-trap captures, no. of camera traps that captured the species, and no. of grid cells in which signs of the species were recorded on transects.

Species	No. of camera trap captures	No. of camera traps (%)	No. of grid cells with carnivore signs (%)
Snow leopard *Panthera uncia*	246	42 (58)	33 (67)
Red fox *Vulpes vulpes*	113	30 (42)	33 (67)
Eurasian lynx *Lynx lynx*	21	9 (13)	7 (14)
Grey wolf *Canis lupus*	2	2 (3)	14 (29)
Dhole *Cuon alpinus*	1	1 (1)	0 (0)
Snow leopard + fox		24 (33)	22 (45)
Snow leopard + lynx		5 (7)	3 (6)
Snow leopard + wolf		2 (3)	11 (22)
Snow leopard + dhole		1 (1)	0 (0)

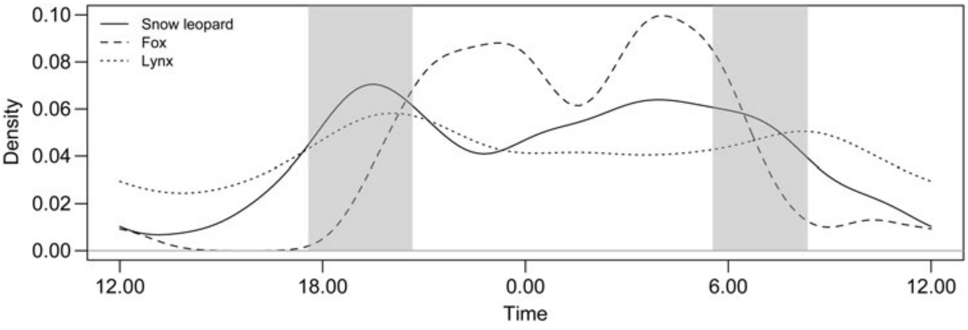

FIG. 3 Activity patterns of the snow leopard, red fox and Eurasian lynx, based on camera trap surveys in Qilianshan National Nature Reserve (snow leopard, n = 246; red fox, n = 113; Eurasian lynx, n = 21), presented as kernel density estimates. The light grey bands indicate sunrise (05.52–08.37) and sunset (17.56–20.48).

(Linkie & Ridout, 2011). Analyses were performed using the package *overlap v. 0.2.4* (Meredith & Ridout, 2014) in *R v. 3.1.3* (R Development Core Team, 2014).

During January–March 2014 we conducted sign surveys along routes that snow leopards were expected to use, within 49 grid cells of a larger area of the Reserve (Fig. 2). Mammalian carnivore sign was recorded in 100 m segments along transects, and categorized according to species. We recorded only tracks that were easily recognizable, identified unambiguously and considered to be recent (< 1 month old), with sharply defined edges and shapes. Multiple signs of the same species in the same 100 m segment were not recorded separately. Signs of snow leopard, lynx, grey wolf and red fox were differentiated on the basis of size, shape and context-specific information; for example snow leopard tracks tend to be larger than those of lynx (Mallon, 1984), although those of a subadult snow leopard are of a similar size to those of an adult lynx (Jackson & Hunter, 1996). We therefore ascribed such smaller tracks to lynx unless they were accompanied by tracks of an adult snow leopard, given that young snow leopards stay with their mothers for an estimated 18–22 months after birth (Jackson, 1996). We did not record canid tracks if signs of human presence were also found in the same area, to avoid recording tracks of domestic dogs.

Results

Cameras were active for a collective total of 8,498 trap days. We obtained 246 captures of snow leopard, 113 of red fox, 21 of lynx, two of grey wolf and one of dhole *Cuon alpinus*. We captured snow leopards at 42 of the 72 (58%) camera trap stations. Red foxes were captured at 30 (42%), lynx at nine (13%), and grey wolves at two (3%) of the stations (Table 1). Red foxes tended to be captured at camera trap stations that also captured snow leopards: 24 camera traps captured both species and accounted for the majority (79%) of fox captures. Lynx also tended to be captured at the same locations as snow leopards, with five camera traps capturing both species and accounting for the majority (67%) of lynx captures.

Snow leopards were most commonly detected in the evening and early night (17.00–21.00), with a peak around sunset (19.00–20.00; Fig. 3). Detections of snow leopards were also common during 01.00–07.00. Captures of red foxes were most common early in the night (21.00–midnight) and in the early hours of the morning (03.00–06.00), peaking during 05.00–06.00. The lynx detection pattern was less obvious because of the small sample size but suggests continuous detections, with a somewhat decreased frequency during the day. The two detections of wolves were at 20.30 and 23.43. Kernel density estimates suggested a high degree of temporal overlap between the snow leopard and the red fox (Fig. 3), as indicated by a high overlap coefficient estimate ($\Delta_4 = 0.72$, 95% CI 0.61–0.78). There was also a high degree of temporal overlap between the snow leopard and the lynx ($\Delta_1 = 0.85$, 95% CI 0.80–0.95) but this should be interpreted with caution given the small number of lynx captures (n = 21).

At the landscape scale a total of 244 km of transects were surveyed within 49 grid cells covering 784 km^2 (Table 1). Snow leopard signs were detected most frequently, occurring in 33 grid cells and on 34% of transects. Signs of red fox were also widespread, detected in 33 grid cells and on 28% of transects. Grey wolf and lynx were detected in 14 (naïve occupancy = 29%) and seven (naïve occupancy = 14%) grid cells, respectively. Concurrent signs of both snow leopard and red fox were detected in 22 grid cells (Table 1). Signs of both snow leopard and lynx were detected in three grid cells, and of both snow leopard and wolf in 11 grid cells.

Discussion

The results of our survey at various scales confirm that other carnivores occur in areas of snow leopard occurrence, albeit with low detection rates for the lynx, wolf and dhole. Even in the smaller scale camera-trap survey all five carnivores (snow leopard, lynx, wolf, red fox and dhole) were observed. These simple relationships suggest there is some potential for the protection of snow leopard habitat to benefit other species. Camera traps recorded snow leopards and lynx using the same travel route at five locations. If, as intimated by these findings, snow leopards and other carnivores share the same travel routes, there is an opportunity to consider protective measures at the local scale that would simultaneously benefit multiple species; for example, preventing the use of poaching traps along such routes or minimizing human disturbances (such as fences and roads) would have multiplier effects on other species. This would be particularly relevant in Qilianshan National Nature Reserve and other areas in China (Xu et al., 2008) where development projects (including road building, mining and hydroelectric dams) are underway. The use of predator-proof corrals (which protect livestock from predation by all carnivores) and better husbandry practices (including control of herding dogs, which often come into conflict with carnivores) should also be encouraged (Aryal et al., 2014; Alexander et al., 2015a).

It is important to recognize that snow leopard conservation efforts could potentially increase the population numbers of carnivores that have a negative impact on local livelihoods. This could lead to exacerbation of livestock depredation and further human–wildlife conflicts. In the study area lynx and wolves are seen as the main culprits of livestock depredation, and their increased numbers could have negative consequences for snow leopards (Alexander et al., 2015a). Umbrella effects of conservation efforts must therefore be taken into consideration not only in terms of potential benefits for other threatened species but also because of the complex interactions inherent in human–wildlife conflict involving an assemblage of carnivore species.

This study is exploratory and further assessments are required to evaluate the ecological significance of sympatric carnivore co-occurrence across these mountain landscapes. Our survey design, which targeted snow leopards, may have led to low capture rates of wolves and lynx, thus limiting inferences on dynamics and interactions. These low rates may also be attributable to lower densities of these species, or differential space use between lynx, wolves and snow leopards. Further studies on interspecific interactions within this carnivore assemblage should attempt to broaden the range of sampling sites beyond those preferred by snow leopards. A non-targeted approach, however, carries a risk of low detection probabilities for all species. We therefore recommend combining information from surveys that target each species of interest. Sign surveys can be carried out over large areas more readily then camera-trap surveys but must be conducted carefully to minimize misidentification of species.

We provide evidence that a number of carnivores share the snow leopard's habitat at multiple scales. This raises the possibility that efforts to conserve the snow leopard could have both positive and unintended negative spill-over effects. Although simple measures could leverage broad-based synergistic impacts among species, complex interactions arising from human–wildlife conflicts could influence final outcomes.

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References

ALE, S.B., YONZON, P. & THAPA, K. (2007) Recovery of snow leopard *Uncia uncia* in Sagarmatha (Mount Everest) National Park, Nepal. *Oryx*, 41, 89–92.

ALEXANDER, J., CHEN, P., DAMERELL, P., YOUKUI, W., HUGHES, J., SHI, K. & RIORDAN, P. (2015a) Human wildlife conflict involving large carnivores in Qilianshan, China and the minimal paw-print of snow leopards. *Biological Conservation*, 187, 1–9.

Alexander, J., Gopalaswamy, A.M., Shi, K. & Riordan, P. (2015b) Face value: towards robust estimates of snow leopard densities. *PLoS ONE*, 10(8), e0134815.

Andelman, S.J. & Fagan, W.F. (2000) Umbrellas and flagships: efficient conservation surrogates or expensive mistakes? *Proceedings of the National Academy of Sciences of the United States of America*, 97, 5954–5959.

Aryal, A., Brunton, D., Ji, W., Barraclough, R.K. & Raubenheimer, D. (2014) Human–carnivore conflict: ecological and economical sustainability of predation on livestock by snow leopard and other carnivores in the Himalaya. *Sustainability Science*, 9, 321–329.

Bhatnagar, Y.V., Mathur, V.B. & McCarthy, T. (2002) A regional perspective for snow leopard conservation in the Indian Trans-Himalaya. Unpublished paper presented at the National Workshop on Regional Planning for Wildlife Protected Areas, 6–8 August 2001, India Habitat Centre, New Delhi, India.

Caro, T.M. (2003) Umbrella species: critique and lessons from East Africa. *Animal Conservation*, 6, 171–181.

Dalerum, F., Somers, M.J., Kunkel, K.E. & Cameron, E.Z. (2008) The potential for large carnivores to act as biodiversity surrogates in southern Africa. *Biodiversity and Conservation*, 17, 2939–2949.

IUCN (2015) *The IUCN Red List of Threatened Species v. 2015.1*. Http://www.iucnredlist.org/ [accessed January 2015].

Jackson, R. (1996) *Home range, movements and habitat use of snow leopard (*Uncia uncia*) in Nepal*. PhD thesis. University of London, UK.

Jackson, R. & Hunter, D.O. (1996) *Snow Leopard Survey and Conservation Handbook*. International Snow Leopard Trust, Seattle, USA, and U.S. Geological Survey, Fort Collins, USA.

Jackson, R., Mallon, D., McCarthy, T., Chundaway, R.A. & Habib, B. (2008) *Panthera uncia*. In *The IUCN Red List of Threatened Species 2008*. Http://dx.doi.org/10.2305/IUCN.UK.2008.RLTS.T22732A9381126.en [accessed 24 September 2015].

Jumabay-Uulu, K., Wegge, P., Mishra, C. & Sharma, K. (2014) Large carnivores and low diversity of optimal prey: a comparison of the diets of snow leopards *Panthera uncia* and wolves *Canis lupus* in Sarychat-Ertash Reserve in Kyrgyzstan. *Oryx*, 48, 529–535.

Karanth, K.U. & Chellam, R. (2009) Carnivore conservation at the crossroads. *Oryx*, 43, 1–2.

Li, J., Schaller, G.B., McCarthy, T.M., Wang, D., Jiagong, Z., Cai, P. et al. (2013) A communal sign post of snow leopards (*Panthera uncia*) and other species on the Tibetan Plateau, China. *International Journal of Biodiversity*, 2013, 370905.

Linkie, M. & Ridout, M.S. (2011) Assessing tiger–prey interactions in Sumatran rainforests. *Journal of Zoology*, 284, 224–229.

Mallon, D. (1984) The snow leopard in Ladakh. *International Pedigree Book of Snow Leopards*, 4, 23–37.

Meredith, M. & Ridout, M. (2014) Package 'overlap'. Https://cran.r-project.org/web/packages/overlap/overlap.pdf [accessed 24 September 2015].

Noss, R.F. (1990) Indicators for monitoring biodiversity: a hierarchical approach. *Conservation Biology*, 4, 355–364.

R Development Core Team (2014) *R: A Language and Environment for Statistical Computing*. R Foundation for Statistical Computing, Vienna, Austria.

Ridout, M.S. & Linkie, M. (2009) Estimating overlap of daily activity patterns from camera trap data. *Journal of Agricultural, Biological and Environmental Statistics*, 14, 322–337.

Rozylowicz, L., Popescu, V.D., Pătroescu, M. & Chişamera, G. (2011) The potential of large carnivores as conservation surrogates in the Romanian Carpathians. *Biodiversity and Conservation*, 20, 561–579.

Sergio, F., Newton, I., Marchesi, L. & Pedrini, P. (2006) Ecologically justified charisma: preservation of top predators delivers biodiversity conservation. *Journal of Applied Ecology*, 43, 1049–1055.

Snow Leopard Network (2014) *Snow Leopard Survival Strategy*. Seattle, USA.

Snow Leopard Working Secretariat (2013) *Global Snow Leopard and Ecosystem Protection Program*. Bishkek, Kyrgyz Republic.

Worthy, F.R. & Foggin, J.M. (2008) Conflicts between local villagers and Tibetan brown bears threaten conservation of bears in a remote region of the Tibetan Plateau. *Human–Wildlife Conflicts*, 2, 200–205.

Xu, A., Jiang, Z., Li, C., Guo, J., Da, S., Cui, Q. et al. (2008) Status and conservation of the snow leopard *Panthera uncia* in the Gouli Region, Kunlun Mountains, China. *Oryx*, 42, 460–463.

Biographical sketches

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