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 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).

METHODS

Study area

The study was carried out on the eastern side of Ruaha National Park (RNP) in southern-central Tanzania (Fig. 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 2,171 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 (Fig. 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 (Fig. 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; Supplementary material Appendix 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).

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 – Mackenzie 2006), by acknowledging that arbitrary choice of occasion length may result in some temporal dependence (assumption 2), and by admitting 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). All 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 three chains of 30,000 iterations each, including 10,000 iteration burn-ins. Model convergence was assessed from both the R-hat value (<1.1 for reliable convergence) and from a 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 (Appendix A). 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 closest detection of the other species in the 10 days before and after (hereafter, proximal detection). If the reference detection was followed by another detection of the same species, it was excluded from the analysis. For each day (n = 20), a detection probability was obtained by dividing the number of proximal detections falling into that day by the total number of detections for the corresponding species (spotted hyaena, dikdik, impala, zebra or giraffe). Graphically, we obtained an empirical detection probability distribution 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 proximal detections occurring within 10 days of reference lion 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 proximal detections for a given species 1000 times to generate expected distributions for each day. Each iteration of the randomisation procedure implemented the following steps for every detection of a species (other than lion): 1) a new date was selected at random from the survey period 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 proximal detections and the unchanged reference 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 $\alpha = 0.05$. All data used in this study are available from the Dryad Digital Repository: http://datadryad.org/resource/ doi:10.5061/dryad.br86d (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 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 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 3). Temporal overlap between lions and each herbivore species varied noticeably, with highest and lowest overlap found with dikdiks and giraffes in both seasons, respectively (Table 3). 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 > 0.01).

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 Supplementary material Appendix 2. 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. 2a). Dikdiks and impalas did not appear to have any notable effect on lion occupancy (Fig. 2b and c). Whilst giraffe occupancy showed a slight tendency to positively influence that of lions in both seasons (Fig. 2e), the effect of zebra was negligible and appeared to vary in direction (Fig. 2d). Choice of occasion length did not 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).

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 (Fig. 3). 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. 3). When an occasion length of five days was used, spotted hyaena detection was positively influenced by prey species 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. Finally, 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 detection probability distributions. Spotted hyaenas and lions were more likely to be detected within one day of each other during the dry season of 2013 (Fig. 4; both $P < 0.05$), but showed no significant bias during the dry season of 2014. 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 (Fig. 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.

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 during the dry season of 2013, our analysis of temporal spacing did not allow us to infer on the direction of this potential behaviour, since both species were found to closely 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.

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). Most importantly, known 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.

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, however, 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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Supplementary material (Appendix oik.XXXXX at www.oikosjournal.org/readers/appendix). Appendix 1– 3.

TABLE LEGENDS

Table 1. Overview of the spatiotemporal approaches implemented in this study.

Method	Description	Outcome	References
Activity pattern overlap	Qualitative assessment of the degree of temporal overlap between the activity patterns of two species	Temporal association	Ridout and Linkie 2009; Meredith and Ridout 2014
Co-occupancy modelling	Quantitative assessment of the influence of one species' occupancy on the occupancy of another, both corrected for imperfect detection	Spatial association	Waddle et al. 2010; Bischof et al. 2014
Co-detection modelling	Quantitative assessment of the influence of one species' binary detection/non-detection on the binary detection/non-detection of another	Spatiotemporal association	
Temporal spacing	Quantitative assessment of the temporal spacing between successive detections of two species at shared camera trap sites	Spatiotemporal association	

Table 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.

				# photographic events		Naïve occupancy		Naïve detection	
Taxonomic group	Latin name	Common name	Mass (kg)[a]	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 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	0.78 [0.67 - 0.88]	0.78 [0.67 - 0.87]
Dikdik	0.65 [0.54 - 0.75]	0.63 [0.51 - 0.75]
Impala	0.31 [0.24 – 0.39]	0.49 [0.38 - 0.59]
Zebra	0.43 [0.35 – 0.52]	0.47 [0.36 - 0.59]
Giraffe	0.29 [0.21 - 0.37]	0.43 [0.33 - 0.54]

FIGURE LEGENDS

Figure 1. Location of camera trap sites within Ruaha National Park (RNP). The inset map shows the location of RNP in southern-central Tanzania.

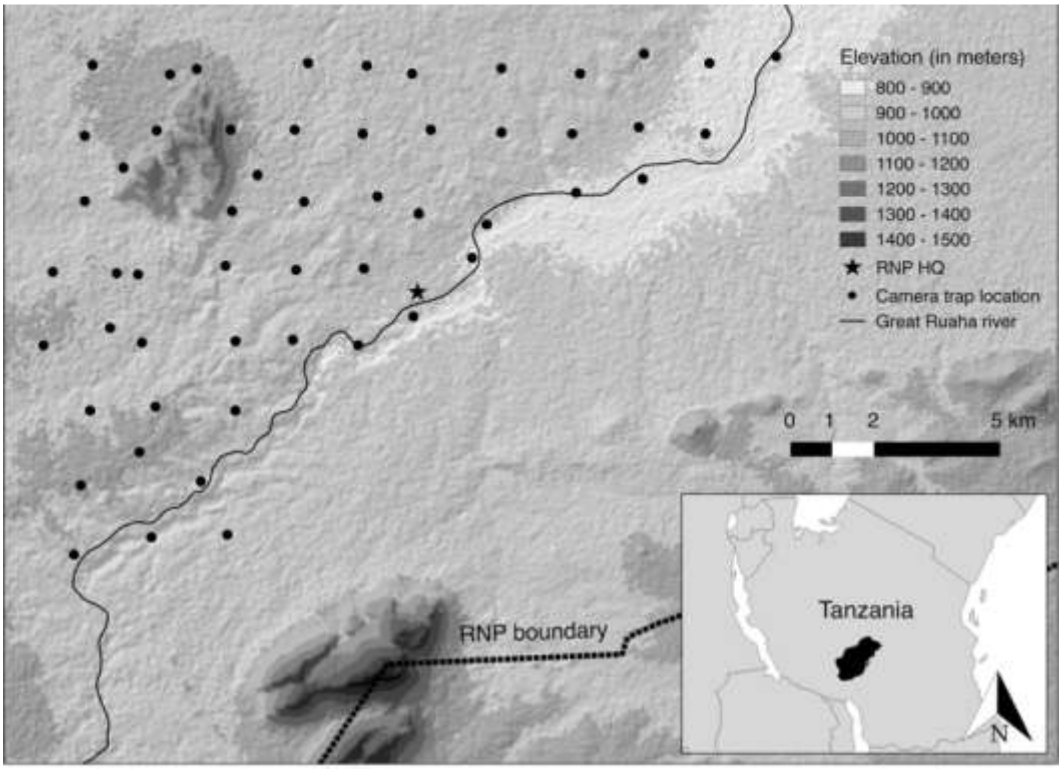

Figure 2. Posterior probability density functions associated with inter-specific effects on probability of occupancy for the dry seasons of 2013 and 2014, as estimated from hierarchical multi-species occupancy models. Occupancy is interpreted as the probability of camera trap site use by a species. Spatial 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.

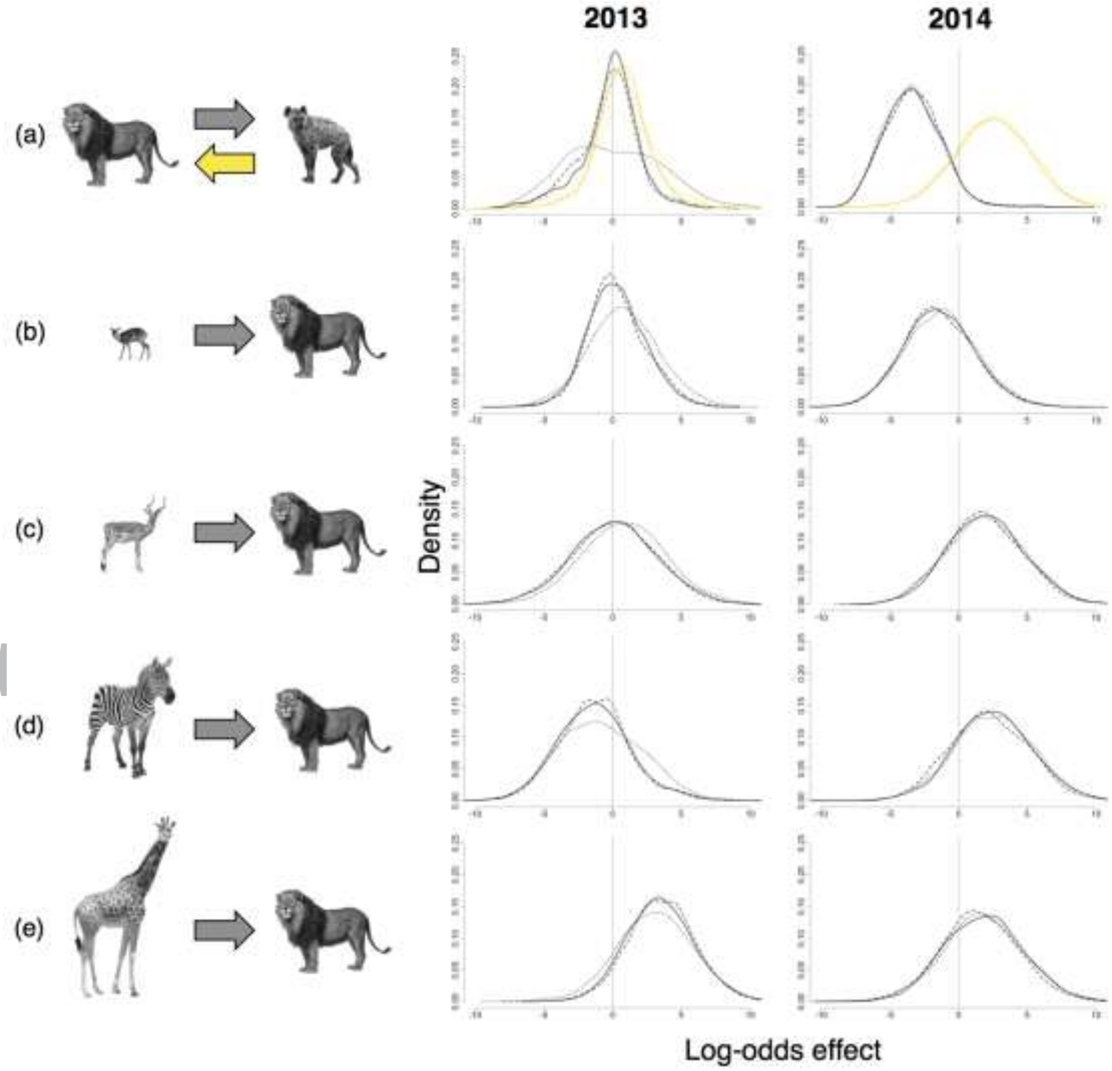

Figure 3. Coefficient estimates and associated standard errors for inter-specific effects on spotted hyaena (top row) and lion (bottom row) detection during the dry seasons of 2013 and 2014. Here, detection is a binary variable describing whether or not the target species was photographed at a given 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.

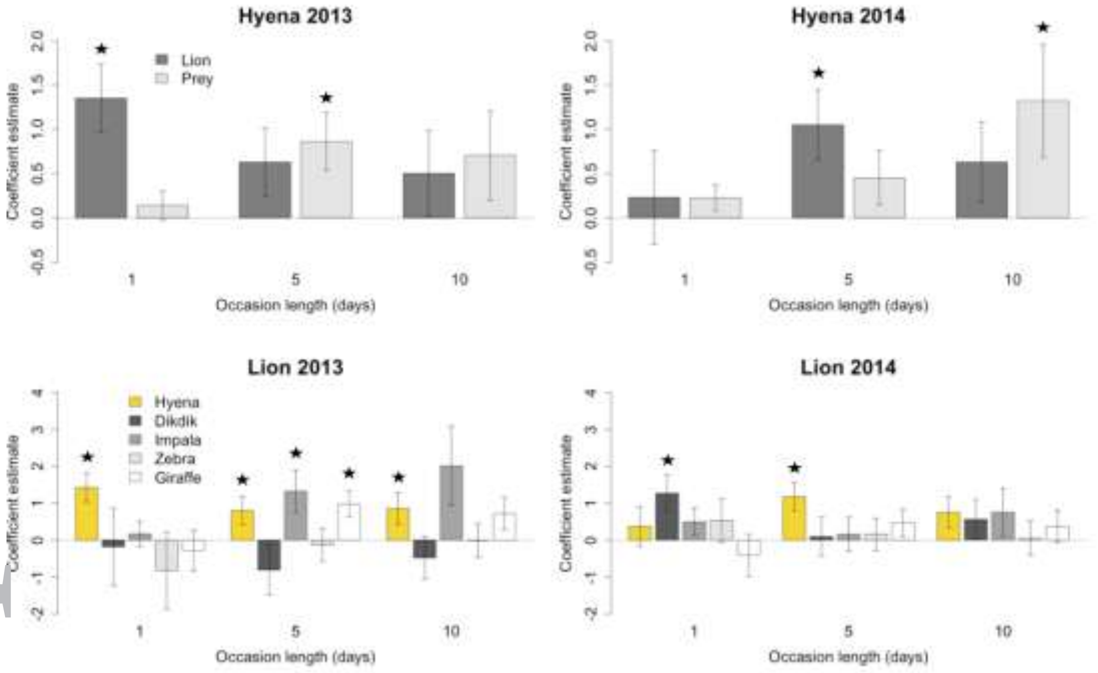

Figure 4. Observed (red) and expected (grey) distributions describing the probability of detecting spotted hyaenas, impala and giraffes for the first time during one to 10 days before and after detection of a lion at the same camera trap. For each day, detection probabilities were obtained by dividing the number of proximal 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 detections for the corresponding species. Asterisks mark days for which observed detection probability was significantly different to expected. Sample sizes used to draw empirical distributions are given in each case. Note, y axes vary.