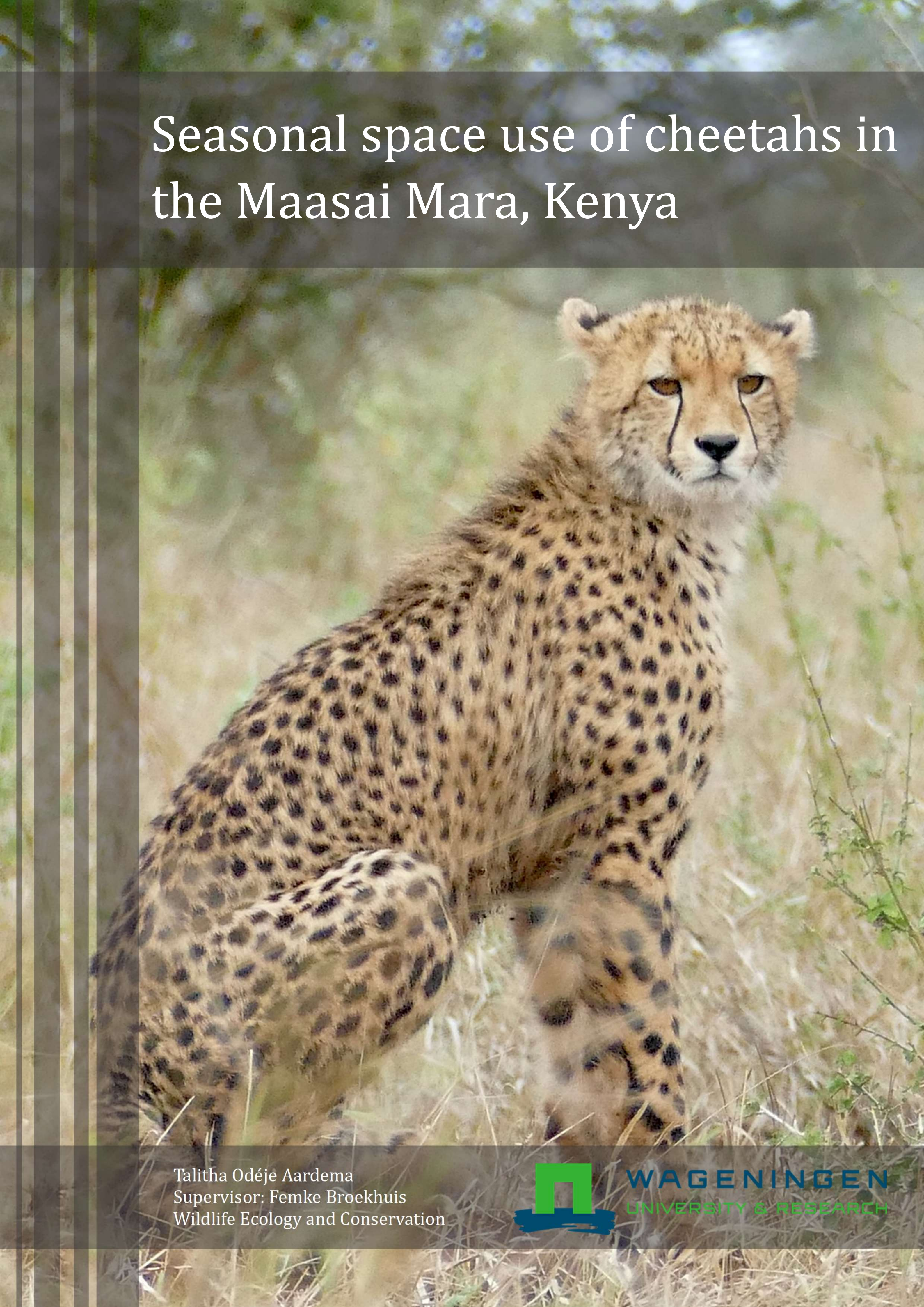
Seasonal space use of cheetahs in the Maasai Mara, Kenya



Talitha Odéje Aardema
Supervisor: Femke Broekhuis
Wildlife Ecology and Conservation

WAGENINGEN
UNIVERSITY & RESEARCH

Seasonal space use of cheetahs in the Maasai Mara, Kenya

Talitha Odéje Aardema

Student number: 1027903

Supervisor: Femke Broekhuis

MSc Wildlife Ecology and Conservation Thesis - WEC80436

Wageningen University and Research

April 2024

Abstract

Background: Space use is an important component of animal ecology and is highly species-specific. It can vary over seasons and be driven by various environmental and anthropogenic factors. The Maasai Mara in Kenya yearly experiences a huge influx of herbivores as the great migration passes through its land, as well as grazing livestock in the area year round, highly impacting the carnivores in the area. However, how exactly this migration impacts the space use of cheetahs in the Maasai Mara has not been extensively studied yet.

Aim: Determine what drives space use of cheetahs out of migration and during migration and whether there is a difference in cheetah space use between these seasons.

Organism: Cheetah (*Acinonyx jubatus*).

Place of research: The Maasai Mara, Kenya.

Methodology: Cheetah sightings data were gathered in 2017 during the season out of migration (February 1st to May 2nd) and the season during migration (August 1st to October 30th), as well as sightings data on livestock and wild prey species. Using R and QGIS, a multi-season occupancy model was applied, analyzing the effect of semi-closed habitat, livestock and wild prey abundance on cheetah occupancy during both out of migration and during migration.

Principal findings: The results showed no significant effects of livestock, wild prey and the proportion of semi-closed habitat on the cheetah occupancy. However, during migration the occupancy of cheetahs was more spread out then out of migration, possibly a result of the high number of wild prey passing through the area.

Conclusion: Large carnivores tend to spread in occupancy during migration as a response to high influx of wild prey. However, a deeper investigation needs to be done in order to find out which factors are driving the difference in occupancy per season, taking in consideration differences between sexes and the temporal and spatial scale.

Correspondence: Dr. Femke Broekhuis – femke.broekhuis@wur.nl

1. Introduction

Space use is an important component of animal ecology and is highly species-specific. A species' choice for a certain habitat or area is among other things dependent on resource availability and risk factors (e.g. anthropogenic factors; Sargent *et al.*, 2022). Space use can be highly variable over seasons and changes throughout the year as resource availability changes (Lakshminarayanan *et al.*, 2016; Hongo *et al.*, 2018). Access to food is one of the most important resources for a carnivore and is, amongst other things, related to prey availability and hunting strategies (e.g. ambush or coursing). In most ecosystems, prey abundance changes over seasons as foraging opportunities shift. Large carnivore species were documented to shift their diet or space use in response to changes in prey densities (Bissett *et al.*, 2012; Arthur & Del Vecchio, 2017; Vettorazzi *et al.*, 2022). Previous research on large felid species, such as the lion (*Panthera leo*) and the snow leopard (*P. uncia*), has shown that seasons, in relation to prey abundance, can influence the extent to which the species make use of a certain habitat (Kittle *et al*., 2016; Xiao *et al.*, 2022). During the wet season in Africa, lions shift their space use to the areas closer to prey in order to cope with the low prey abundance (Kittle *et al*., 2016). They make use of the embankments next to watering holes to catch the few available prey by ambushing them. In the dry season they were often seen at the limitedly available watering holes, as most prey was present in these areas. Snow leopards also show seasonal differences in habitat use (Xiao *et al.*, 2022). In summer, snow leopards tend to utilize habitats at higher elevations, as this is where their prey moves during this season.

In multiple big cat species, seasonal variation in space use is not just explained by varying prey abundance, anthropogenic factors play a crucial role in space use as well. In most cases predators seem to avoid human disturbance in certain seasons, as closely sharing space with humans and livestock often results in a lower abundance of wild prey, due to competition for resources (Xiao *et al.*, 2022). Human-predator interactions can also result in direct conflicts, with guarding dogs or pastoralists, which may eventually lead to injuries or even death for the predators (Xiao *et al.*, 2022; Zanón Martínez *et al.*, 2023). On the other hand, the presence of livestock also presents an opportunity of catching relatively easy prey. When there are periods of low prey abundance, various carnivore species such as lions, leopards (*P. pardus*), spotted hyenas (*Crocuta crocuta*), jaguars (*P. onca*) and wolves (*Canis lupus lupaster*) have shown to predate on livestock (Kissui, 2008; Atickem *et al.*, 2017; Igor *et al.*, 2015). When wild prey abundance is low, large carnivores might come closer to livestock areas to predate on livestock as an alternative food source. In Kenya, livestock movement through the wildlife areas varies per season (Butt, 2010). Similar to the wild herbivores, pastoralists in the area try to find the best grass patches for their livestock, varying per season. A study by Kissui *et al.* (2008) found that lions killed more livestock when out of the migration (low prey abundance) compared to during the migration (high prey abundance). However, not only low wild prey abundance affects the extent of livestock depredation. In certain areas, pastoralists relocate their livestock according to the environmental circumstances. This creates a seasonal fluctuation in pressure on the ecosystem by grazing livestock, seasonally impacting the predators in the system as the livestock shares resources with the wild prey species (Schooler *et al.*, 2022).

In the Maasai Mara in Kenya, wild prey abundance is a hugely seasonally fluctuating factor as the great migration passes through its grounds every dry season, bringing in over a million herbivores (Holdo *et al.*, 2009). The huge influx of available prey might be a driver for large carnivores to change the way of making use of the resources in an area. They might shift in prey in response to the seasonally available prey species or they might use different habitats to gain the highest hunting success (Mills *et al.*, 2004).

Cheetahs (*Acinonyx jubatus*) generally use the more open areas, such as plain grass fields, to hunt and more densely vegetated areas to rest (Purchase & Du Toit, 2000). As cheetahs are coursing predators, reliant on their speed to catch prey, the open plains present them the most opportunities for successful hunting (Gigliotti *et al.*, 2020). A previous study by Klaassen and Broekhuis (2018) has shown that semi-closed habitats are important for cheetahs as well, possibly because this habitat allows them to remain undetected by other predators. In a study by Vettorazzi *et al.* (2022), cheetahs showed a wider prey profile out of the wildebeest migration compared to during the migration. As there is a lower prey density out of the migration, cheetahs might be forced to widen their prey spectra in order to meet their dietary requirements and therefore use a higher variety of habitats (Mills *et al.*, 2004). This could lead to predation in less suitable habitats where chasing prey is more difficult, such as densely vegetated areas and making less use of the more preferred semi-closed habitat during the season with a low wild prey abundance.

In this research, I will study whether there is a seasonal variation in cheetah space use in the Maasai Mara. It is known that carnivores focus on wild prey species and livestock in different seasons, however, it is still unknown if this has an influence on their space use over seasons. In more extensively studied big cat species, the main drivers for seasonal variation in space use are, amongst other factors, related to wild prey availability and anthropogenic factors, including livestock density (Schooler *et al.*, 2022). In this study, I will therefore focus on these components to examine whether these explain possible variation in cheetah space use during a period of high prey density (migration) and a period of low prey density (out of migration). I expect cheetahs to use more of their overall preferred habitat, the semi-closed habitat, during the migration. In this period a high abundance of prey species is present for the cheetah. Out of the migration, the lower abundance of wild prey might force cheetahs to catch wild prey in less suitable areas, such as more densely vegetated areas. I therefore expect a stronger selection for more the semi-closed habitats during the migration than out of the migration. I hypothesize that wild prey abundance drives a seasonal difference in cheetah space use. I expect the abundance of Thomson's gazelle (*Eudorcas thomsonii*) and wildebeest (*Connochaetes taurinus*), both migratory species in the Maasai Mara, to positively influence the cheetah occupancy. I expect to find this mainly during the migration, as their abundances are highest during this season. Considering livestock, I expect cheetahs to not adapt their space use in response to livestock abundance during the migration. In this period enough wild prey is present to risk taking livestock as prey. Out of the migration, the number of wild prey is lower, possibly forcing cheetahs to predate on livestock to feed. I thus expect livestock abundance to positively affect cheetah space use out of migration.

2. Methods

2.1 Study area

The data for this study were gathered in the Maasai Mara, which is situated in the South-West of Kenya, next to the border of Kenya-Tanzania and in adjacency to Serengeti National Park (Fig. 1). The study area includes the Maasai Mara National Reserve, the Mara Triangle and multiple adjacent wildlife conservancies, which is an area of about 2,400 km^2 (Broekhuis *et al.*, 2021). The Maasai Mara is a heterogeneous landscape. Its habitat types vary from short grassland to tall grasslands and shrublands to forests (Oindo *et al.*, 2003). The study area yearly experiences multiple dry seasons and wet seasons. The dry season stretches from July to October and the wet season from November to December (short rains) and from March to June (long rains; Ogutu et al. 2008). Rainfall in the wet season triggers the vegetation growth over the entire system. Each year during the dry season, around August, large numbers of wildebeest, zebra (*Equus quagga*) and Thomson's gazelle migrate from the Serengeti, Tanzania, to the Maasai Mara in search of food and water. This results in an increase in prey abundance for the large carnivores which reside in the Maasai Mara, such as cheetahs, lions, spotted hyenas and leopards (*Panthera pardus*).

In and around the surrounding conservancies, at the Northern and Eastern border of the Maasai Mara National Reserve, pastoralists graze with their livestock in a semi-nomadic way (Butt *et al.*, 2009). They graze with their livestock according to the availability of resources in the area and relocate their herds from time to time to temporary enclosures (Butt *et al.*, 2009). The livestock in this area consists of cattle, sheep and goats, which have highly increased in number over the past decades, mostly ascribable to the number of sheep and goats (Ogutu *et al.*, 2016).

2.2 Data collection

2.2.1 Sightings data

The sightings data I used in this study were sightings data from the Maasai Mara (Broekhuis *et al.*, 2021). These data were collected using the methods described by Broekhuis and Gopalaswamy (2016). In short, the data were gathered by driving around and recording the sighted species (e.g. carnivore and herbivore species and livestock) using the software Cybertracker. The number of individuals of each species at the

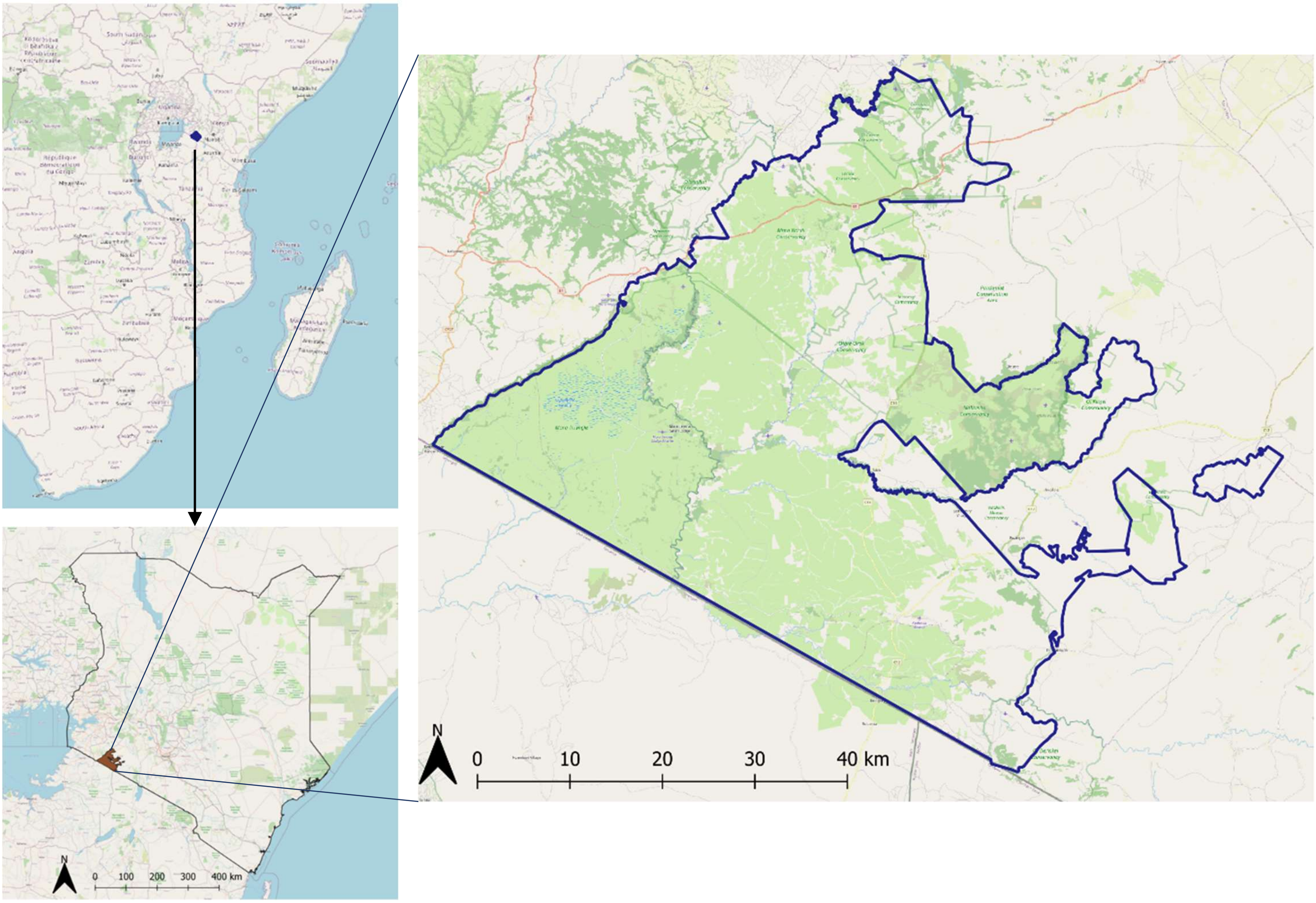


Figure 1 - A map of the study area, the Maasai Mara, Kenya. This map was created using QGIS software (QGIS Development Team, 2021).

sighting was also documented. Additional information at the moment of the sighting of vehicles or animals was incorporated in the dataset as well, such as the observer(s), the day, the time and the GPS location of the sighting. The data were collected over timespan of multiple years, and in this study I used the data gathered in 2017. Of this year, I selected the cheetah as main study species. As a proxy for the wild prey abundance, I chose the wildebeest and Thomson's gazelle sightings as covariates. The wildebeest and gazelle sightings were used separately as a species to evaluate their individual effect on cheetah occupancy. The sightings of the livestock species, which included cattle, sheep and goats, were also included as a covariate. I used the data collected in two time slots (surveys) of each 90 days and selected one survey during the migration (August 1st – October 30th) and one survey outside the migration period (February 1st – May 2nd). During each survey, the amount of effort, indicating the number of kilometers driven during the data collection, was documented per day. The effort data consist of GPS-routes, which were used to calculate the amount of kilometers driven per survey using QGIS 3.4 (QGIS Development Team, 2021). This GPS-data were also used to calculate the amount of kilometers driven in each grid cell during each season.

2.2.2 Habitat data

The habitat data I worked with were created by Broekhuis *et al.* (2017). A habitat structure map was created to show the habitat types in the study area. It is based on two LandSat 8 satellite images from July 2013 and January 2014. Using the software R 2.14.2 (R Development Core Team, 2016) and QGIS v2.8.4 (QGIS Development Team, 2015) the method 'Random Forest' was applied to classify the different habitats, as this yielded a high classification accuracy.

The habitat data were categorized in five separate land types. The three main habitat structure components were: open habitat, including bare ground and grasslands, semi-closed habitat, including shrubs, bushes and acacia woodland and a closed habitat, which covers dense vegetation. This dense vegetation mostly consists of trees (Broekhuis *et al.*, 2017). The two less common land types were water and agricultural areas.

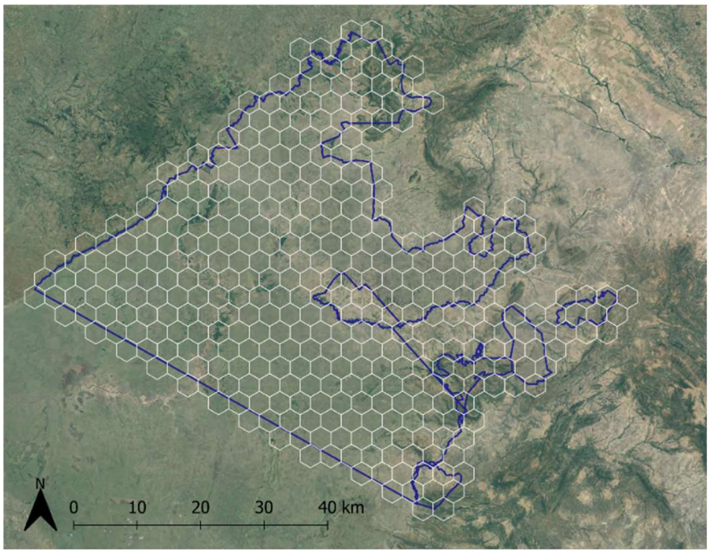


Figure 2 - The hexagon grid and the study area. The blue contours indicate the boundaries of the study area and the white hexagons show the hexagon grid cells ('sites'). The grid consists of 373 hexagons, which cover 9 km^2 each. This map was created using QGIS software (QGIS Development Team, 2021).

In the analysis only the proportion of semi-closed habitat in each grid cell was used (9 km$_2$), as previous research found that this habitat type is the most preferred by cheetahs (Klaassen & Broekhuis, 2018). Using the proportion of semi-closed habitat is most useful to examine the effect of seasons and habitat type on the space use by cheetahs, as I expect cheetahs to show the strongest response to this habitat type.

2.3 Occupancy analysis

Using multi-season single-species occupancy models of the package '*unmarked*' in the software R version 4.3.1 (Fiske & Chandler, 2011; Kellner *et al.*, 2023; R Developmental Core Team, 2023), I analyzed the data to determine whether there is variation in cheetah space use during and out of the migration, driven by livestock abundance, wild prey abundance or habitat type.

Table 1 - Covariates added in the multi-season occupancy model. The covariates are subdivided in detection covariates and occupancy covariates. A minus-sign indicates a negative effect of the covariate on the detection or occupancy probability is hypothesized. A plus-sign indicates a positive effect of the covariate on the detection or occupancy probability is expected. The double plus-sign indicates that a stronger effect is expected.

	Description	**Hypothesized relationship with cheetah occupancy**	
		In Migration	Out of Migration
Detection covariates (p)	**Covariates possibly influencing the detection probability of cheetahs.**		
Semi-closed habitat	The proportion of semi-closed habitat in a grid cell.	**-**	**-**
Effort	The amount of kilometers driven during the survey.	**+**	**+**
Occupancy covariates (Ψ)	**Covariates possibly influencing the occupation probability of cheetahs.**		
Semi-closed habitat	The proportion of semi-closed habitat in a grid cell.	**+**	**-**
Wildebeest	The number of wildebeest per grid cell per sampling occasion, corrected by effort.	**++**	**+**
Gazelle	The number of Thomson's gazelle per grid cell per sampling occasion, corrected by effort.	**++**	**+**
Livestock	The number of livestock per grid cell per sampling occasion, corrected by effort.	**0**	**+**

2.3.1 Input data

To build the model, first the input datasets were created. A hexagon layer was made on top of the study area to divide the study area into 'sites' (Fig. 2). For the hexagon layer I selected an area of 9 km^2 per hexagon (Equation 1), as this allowed me to evaluate the effect of both prey and livestock abundance on the space use of cheetahs. Choosing a larger hexagon size could result in the loss of accuracy in cheetah sightings. It could be that the cheetah is present in only a small part of the hexagon and by enlarging the cell size, this information is lost. On the other hand, choosing a smaller hexagon cell size leads to a large amount of NAs, as not all sites in the study area were covered during the data collection. In total, the hexagon layer consisted of 373 hexagons. The hexagons were merged with the recorded GPS-locations of the cheetahs in R using the function 'over' from the '*sp*' package. Some hexagons were left out of the analysis, as no surveys were performed in these hexagons and the corresponding cheetah data and livestock and wild prey abundance variable were lacking.

Equation 1:

Area hexagon: $\frac{(3\sqrt{3s^2})}{2} = 9$ km^2, where s corresponds with the side length of the hexagon. In my study s = 3.46 km.

To produce the cheetah dataset for the occupancy model, the primary survey periods were divided into 13-day sampling occasions. This resulted in 7 sampling occasions in total. To create the right data format for the modelling, the number of columns equaled the number of sampling occasions plus a column with the site ID, corresponding to a hexagon on the hexagon layer. Each row consisted of a single site ID. Per combination of sampling occasion and site ID there could be three possible outcomes: 1, indicating a sighted cheetah; 0, indicating no cheetah has been sighted in this site; NA, meaning no effort was done at this site (no data collected). In case of a NA, no conclusion could be made about presence/absence of cheetahs at this site during this particular survey.

For the site and yearly covariates (Table 1), a new dataset was created as well. One column contained the site IDs of each site, matching with the ID of the hexagon grid cells and another column contained the proportion of semi-closed habitat in each grid cell, which was considered similar for each season. This was done as I did not expect the habitat type to change over the seasons. The next two columns in the dataset consisted of the kilometers driven in each grid cell in each season, also referred to as the effort. The next 4 columns in the dataset contained the abundance of wild prey. Two of these column contained the gazelle abundance for both seasons and the other two the wildebeest abundance for both seasons. The last two columns in the dataset consisted of the livestock covariate for each season. The wild prey covariate and the livestock covariate were calculated using the number of observed wild prey or livestock in a certain grid cell during the data collection (see 'Sightings data'). The covariate was then corrected by the number of kilometers driven (effort) in a grid cell per season. In this wild prey and livestock data, NAs were used to indicate the absence of effort in certain grid cells during an entire season. Some sites in the hexagon grid lacked effort during both seasons, resulting in just NAs. These hexagons were left out of the analysis, as they added no information to the model.

2.3.2 Occupancy model

Occupancy models are used in ecology to gain more insight in the space-use of species through time, if surveys are repeatedly executed at the same sites. In this project, I used the multi-season occupancy model, which incorporates occupancy probability (Ψ), detection probability (p), extinction (ε) and colonization (γ) in the occupancy model (MacKenzie *et al.,* 2002; MacKenzie *et al.,* 2003).

The model uses both detection probability (p) and occupancy probability (Ψ) to evaluate the occupancy of a species (Mkonyi *et al.*, 2018). The detection probability, p, is the probability a cheetah is detected if it is present at a certain site during the survey. The occupancy probability in the model, Ψ, is the probability the cheetah uses a certain site during the survey. In this study, I used the proportion of semi-closed habitat and effort as covariates possibly affecting the detection probability and the proportion of semi-closed habitat, gazelle, wildebeest and livestock abundance as covariates possibly influencing cheetah occupancy (Table 1).

In the cheetah survey data, the sites were either occupied (1), when the species was detected, not detected (0) but present (e.g. hiding in the bush; false negative), or unoccupied (0). The occupancy model considers three assumptions: (1) No false positives errors are made, e.g. a cheetah cannot be detected when it is not present; (2) Surveys done at a certain site during the same season (primary survey period) are independent; (3) The occurrence state of a cheetah remains similar within all secondary surveys of one season at a certain site, meaning a species either occupies a site or not during a season (MacKenzie *et al.*, 2002). However, a multi-season occupancy model does allow variation in occupancy states throughout a season, .

2.3.3 Multi-season occupancy model

In a multi-season occupancy model, the occupancy states of sites are assumed to be dynamic, unlike in a single-season occupancy model, in which the occupancy state of a site is assumed to be constant throughout the study period. The multi-season model is based on a maximum likelihood method by MacKenzie *et al.* (2003). Whereas a single-season model considers the site occupation to be constant over time, the multi-season model considers local extinction and colonization at the sites as well (Equation 2).

Equation 2:

$$\text{Occupancy probability} = \Psi + p + \varepsilon + \gamma$$

In which Ψ represents the initial occupancy coefficient, p the detection coefficient, ε the epsilon coefficient, indicating extinction, and γ the gamma coefficient, referring to colonization.

Extinction, ε, and colonization, γ, are additional parameters used to model the sightings data in a multi-season occupancy model. The extinction probability is the probability that a certain site which is occupied at time *t*, will be unoccupied at time *t*+1. The colonization parameter determines the probability that a certain site which is unoccupied at time *t* will be occupied at time *t*+1.

2.3.3 Model selection and predictions

The data were analyzed in R using the package '*unmarked*' (Fiske & Chandler, 2011; Kellner *et al.*, 2023) for multi-season occupancy modelling. First, all different combinations of covariates were modelled in the detection model, using only the detection formula and by keeping the other parameters constant. Using the package '*AICcmodavg*', the detection models were ranked based on the Akaike's Information Criterion, the AIC-values. The model with the lowest AIC-value was selected and used in the final modelling. Per coefficient, all combinations of covariates and parameters were modeled and the best models were selected based on their delta AICc value (delta AICc < 2). The best outcomes for each coefficient were then used to build the final model, which was again selected based on the criteria of a delta AICc < 2. At last, predictions were made based on the best explaining model. This was done to predict cheetah occurrence probability per site for each season in the study area, including the naïve occupancy per season.

3. Results

To determine the drivers of cheetah's space use, a multi-season occupancy model was applied using three different categories of covariates: proportion of semi-closed habitat, wild prey abundance and livestock abundance.

Both out of and during the migration, an average of about 12,281 kilometers was driven (during migration 12,238 km, out of migration 12,324 km). The number of sighted cheetahs was comparable over seasons, with 113 cheetah sightings during migration and 114 cheetah sightings out of migration. Of the 373 created sites, 309 were sampled in both seasons and were used in the analysis. Of the 309 sites in total, 60 sites were occupied by at least one cheetah out of migration and 76 sites were occupied by at least one cheetah during the migration. In total, 109 unique sites were occupied by cheetahs in both seasons. Of the 309 sites in the study area, 33 were solely occupied out of migration and 49 sites were solely occupied during migration. A higher overall occupancy probability was seen during the migration, as the naïve occupancy probability went from 0.85 (SE = 0.099) out of the migration to 0.91 (SE= 0.075) during the migration (Fig. 3; Fig. 4).

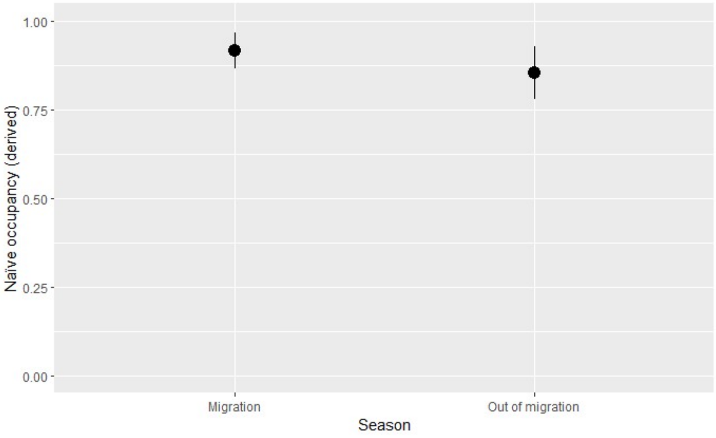


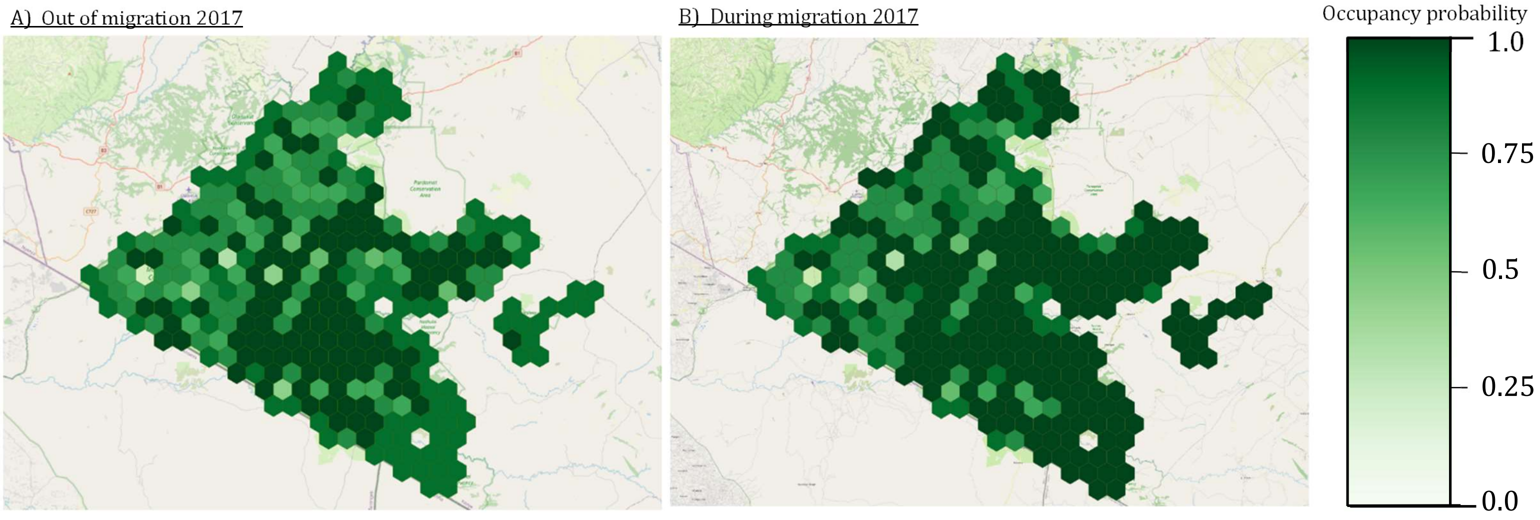
Figure 3 - Naïve occupancy out of migration and during migration. Standard errors have been indicated by the lines along the dots.

3.1 Detection model

In the best performing detection model both effort and the proportion of semi-closed habitat showed a significant positive impact on the detection probability of cheetahs, with effort explaining most variation in the data (Table 2). With effort and semi-closed habitat included in the model, the effort estimate was 0.054 (p-value < 0.001, SE = 0.007; Fig. 5A) and the proportion of semi-closed habitat estimate was 0.17 (p-value = 0.64, SE = 0.36; Fig. 5B).

3.2 Multi-season occupancy models

Ten out of the final 31 models had a ΔAICc value below 2 (Table 2). The weight of these ten models added up to 0.66. The multi-season occupancy model containing semi-closed habitat as


A) Out of migration 2017

B) During migration 2017

Figure 4 - Occupancy maps covering the occupancy probability per site in the study area. A) Occupancy map containing the occupancy probability out of migration. B) Occupancy map containing the occupancy probability during migration. The darker hexagon cells indicate a higher occupancy probability and the lighter cells indicate a lower occupancy probability. The map is based on the best performing model (Table 2).

colonization covariate and effort and semi-closed habitat as detection covariates had the lowest AICc value of 1264.6. However, the weight of this model is relatively low, only 0.11. The Mackenzie-Bailey goodness-of-fit test, which was applied to this model, showed no lack of fit. However, it did indicate under-dispersion in the model ($\hat{c}$ = 0.55).

The initial occupancy (Ψ) in the multi-season models was best explained by the models which included no covariates in the occupancy formula. Only one model in the line-up of models with ΔAICc < 2 included the semi-closed habitat percentage as a covariate in the initial occupancy formula, model 5 (Table 2). The corresponding estimate was 2.85, with a p-value of 0.37 (SE = 3.18), which does not show an effect of semi-closed habitat on the initial cheetah occupancy.

The extinction parameter was generally mostly affected by livestock over the seasons (four out of ten best models). However, even the best models did not show an significant effect of livestock on extinction (p-value = 0.66, SE = 30). Semi-closed habitat was present in the extinction formula in the best models as well, even though this too did not result in significant effects on the extinction coefficient (p-value = 0.60).

The colonization parameter in the study area was best explained by semi-closed habitat (Model 1 in Table 2), even though no significant effect was shown. The 'livestock' and 'gazelle' covariate were present in the colonization formula in a few of the best performing models (gazelle p-value = 0.75; livestock p-value = 0.75). However, they did not show an effect on the colonization coefficient in the models.

The 'wildebeest' covariate was not present in any of the best performing models, so this variable did not show any significant effect on the overall cheetah occupancy in either season.

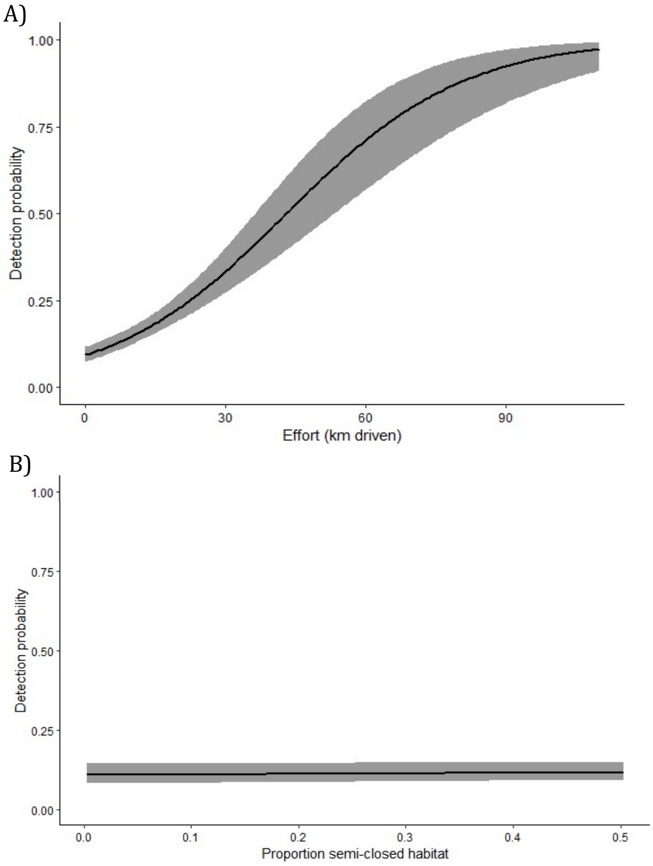


Figure 5 - Predicted relationship between detection probability and the detection covariates. A) The predicted relationship between effort and the detection probability of cheetahs. B) The predicted relationship between the proportion of semi-closed habitat and the detection probability of cheetahs. The black line corresponds with the posterior mean and the grey area represents the 95% confidence intervals.

Table 2 - Model line-up containing the best explaining models. The model selection is based on the ΔAICc value. All models with a ΔAICc value < 2 have been selected. The parameters used in the different formulas are shown in an equation below. The dots indicate no covariates have been used and the formula is kept constant.

Model Line-up	Formula	ΔAICc	AICc Weight
Detection model (p)			
1	Ψ(.) + p(Effort + Semi-Closed Habitat) + ε(.) + γ(.)	0.00	0.5
2	Ψ(.) + p(Effort) + ε(.) + γ(.)	0.03	0.5
Occupancy model (Ψ)			
1	Ψ(.) + p(Effort + Semi-Closed Habitat) + ε(.) + γ(Semi-Closed Habitat)	0.00	0.11
2	Ψ(.) + p(Effort + Semi-Closed Habitat) + ε(.) + γ(.)	0.30	0.21
3	Ψ(.) + p(Effort + Semi-Closed Habitat) + ε(.) + γ(Livestock + Semi-Closed Habitat)	0.65	0.29
4	Ψ(.) + p(Effort + Semi-Closed Habitat) + ε(Livestock) + γ(Semi-Closed Habitat)	1.01	0.36
5	Ψ(Semi-Closed Habitat) + p(Effort + Semi-Closed Habitat) + ε(.) + γ(.)	1.37	0.42
6	Ψ(.) + p(Effort + Semi-Closed Habitat) + ε(Livestock + Semi-Closed Habitat) + γ(.)	1.56	0.47
7	Ψ(.) + p(Effort + Semi-Closed Habitat) + ε(Livestock) + γ(.)	1.57	0.52
8	Ψ(.) + p(Effort + Semi-Closed Habitat) + ε(.) + γ(Gazelle)	1.78	0.57
9	Ψ(.) + p(Effort + Semi-Closed Habitat) + ε(Livestock + Semi-Closed Habitat) + γ(Livestock + Semi-Closed Habitat)	1.81	0.61
10	Ψ(.) + p(Effort + Semi-Closed Habitat) + ε(.) + γ(Gazelle + Semi-Closed Habitat)	1.90	0.66

4. Discussion

In this study I examined whether cheetah occupancy differs between the season out of migration and the season during migration. I studied how cheetah space use in the Maasai Mara is affected by the proportion of semi-closed habitat, wild prey abundance and livestock abundance. Even though no significant differences in cheetah occupancy were found in relation to these parameters, the results display a difference in occupancy from out of migration to migration. The overall occupancy appears to increase from out of migration to during migration, when a high abundance of wild prey arrives in the Maasai Mara. This indicates a higher spread in cheetah occupancy when a large amount of prey passes through the area and a more concentrated cheetah occupancy in times of low prey abundance. During these times of low prey abundance predators are more focused on the fewer concentrated gatherings of prey species, for example close to watering holes (Schooler *et al.*, 2022).

4.1 Sexes

An argumentation why no effect of either habitat type or wild prey abundance on space-use by cheetahs was shown, are the characteristics of different cheetah sexes. Male and female cheetahs tend to respond very differently to their surroundings (Broekhuis *et al.*, 2021). For example, females and young independent cubs are most likely to select more densely vegetated habitats compared to males, who tend to select more open habitats (Welch *et al.*, 2015; Bissett & Bernard, 2007). According to a study by Bissett and Bernard (2007), a more dense habitat type provides a cover for the more vulnerable females and young cheetah cubs. In this way they are less exposed to other predators. Males, especially coalitions, tend to utilize less of the more densely vegetated areas, possibly because they need to meet their higher dietary requirement and hunt more often on the open fields (Bissett & Bernard, 2007). As both sexes select different habitat types, the effect of just one habitat type, in this study the semi-closed habitat, could have gone unnoticed as the males choose other habitats. This may have resulted in no detectable relationship between the proportion of semi-closed habitat and cheetahs' space use.

In this study, the occupancy models did not show any effect of wild prey abundance on cheetah occupancy during both seasons, even though I expected both the gazelle and wildebeest abundance to affect cheetah colonization in the occupancy model. The non-detected influence of wild prey abundance could again be a result of the negligence of the different sexes in the cheetah sightings data in the model. According to various studies, solitary male cheetahs and male coalitions are able to take down large prey, which is why they mainly predate larger prey species, such as wildebeest (Bissett & Bernard, 2007). In contrast to males, females focus mainly on smaller prey species, such as Thomson's gazelle (Broekhuis *et al.*, 2018; Tambling *et al.*, 2014), possibly to avoid injury risk or kleptoparasitism (Hilborn *et al.*, 2018).

Previous studies have documented that cheetahs in the Maasai Mara and the Serengeti adjust their space use in response to wild prey abundance (Broekhuis *et al.*, 2021; Durant *et al.*, 1988). This is mostly limited to female cheetahs and non-residential males, as resident males each have their own territory. However, when prey availability drops and females leave, some males tend to leave their territory (Caro & Collins, 1987). Even though some males have been documented to leave their territories for some time, restriction to territories of residential males could be an explanation why no effect of wild prey abundance on cheetah space use over seasons was found. Residential male cheetahs might not be able to track the high prey abundance as it could mean crossing other cheetahs' territories.

Taking sexes as another component of the model might have resulted in different outcomes, as previous research found different behaviours in females and males. However, by segregating the sexes, the sample size will be strongly reduced, making it more challenging to create well-fitting models which are able to converge.

4.2 Spatial scale

In this study, the parameters were all dependent on the spatial scale. In this study, the chosen spatial scale was 9 km^2, which is quite a broad scale. The lack of effect of covariates on cheetahs occupancy in my results is partially attributable to the large spatial scale. As the scale is broad, it could be that wild prey or livestock is incidentally present at the same sites as cheetah, without the cheetahs deliberately tracking them. The local interactions with other species in the area might be difficult to detect using a large spatial scale, as has been suggested by previous research on large carnivore interactions as well (Dalerum *et al.*, 2020). Previous studies by Morato *et al.* (2018) and Dalerum *et al.* (2020) both approached carnivore modelling studies by selecting multiple spatial scales, to also take in account what affects what at each spatial scale (e.g. home range and foraging scale). This provides information on the interactions on several spatial scales.

As cheetahs use multiple types of habitat, the effect of just one habitat type might not be shown. It might be that all habitat is suitable for cheetahs, as each habitat provides a different purpose for cheetah, for example closely vegetated areas to take refuge and the more open areas to hunt. These ecological justifications are in line with the results of the analysis, suggesting the proportion of semi-closed habitat has no detectable effect on cheetah occupancy, not over seasons as well. On the other hand, my results are in contrast with previous studies done on other carnivore species, such as lions, showing that habitat type is an important driver of their space use (Midlane *et al.*, 2014). However, the study by Midlane *et al.* (2014) was performed on a much broader scale compared to this study, as they used a grid cell size of about 200 km^2. In a study by Klaassen and Broekhuis (2018), they found that cheetahs preferred to use semi-closed habitat. In this study, they used a much finer scale than in my study (30 m^2), allowing them to find interactions at a local level.

The spatial scale is an important factor to consider in occupancy studies, as it can provide an insight on both the fine and the broad scale interactions in an ecosystem (Viana & Chase, 2019). A study by King *et al.* (2021) on carnivores, found that broad spatial scales are able to provide the best understanding of the effect of abiotic factors on a species. The biotic factors, which includes prey, habitat and livestock, were found to be more important driving factors for species at a finer scale (King *et al.*, 2021). Having used a broad spatial scale, the effect of the biotic factors might not have been detected in my study, even though they might have been present. For future research, it would be useful to apply an occupancy model using multiple scales, to get a deeper understanding of interactions at various spatial scales (Kleiven *et al.* 2023).

4.3 Temporal scale

My prediction that livestock abundance drives a shift in cheetah's space use, was not confirmed for either season. Livestock and wild prey abundance did not seem to affect cheetah's space use in the model for either season. An explanation for the non-detected effect of livestock and wild prey abundance on cheetah occupancy might be related to the approach used in this research. To study the effect of livestock and prey on cheetahs, I calculated the livestock abundance, as well as the wild prey abundance, per season as a whole. This is a long time span to detect a possible effect of livestock on cheetahs, as one season covers about three months. Using this large temporal scale, I might not have been able to capture a possibly existing effect of either livestock or prey on cheetah space use. Especially considering that the livestock is moved through the area to find the best grazing grounds on a frequent basis (Butt *et al.*, 2009). On the other hand, previous research by King *et al.* (2021), did not find an effect of the temporal scale on the detection of interactions. This could be because they made use of a two-species model, in which the data on both species have the same temporal scale. This is not the case in this study, where the cheetah data are used with a finer temporal scale compared to the livestock and wild prey data. In my study, the difference in temporal scale between the cheetah data and the prey covariates might have affected the results.

Calculating the livestock and wild prey covariates in multiple time steps (e.g. per sampling occasion, 13 days), might result in more accurately capturing the cheetah-livestock and the cheetah-wild prey interaction, since this provides a more dynamic approach. This could be executed in the form of a multi-species occupancy model (Rota *et al.*, 2016). However, this model considers the absence and presence of prey and the study species per survey rather than abundance per season. The abundance of prey will partially be translated into occupancy, as migratory prey species, such as gazelle and wildebeest, are likely to occur in more 'sites' in the study area during migration than out of migration, considering their yearly movement pattern. A multi-species occupancy model might be able to provide a deeper understanding of the relationship between cheetah and prey species' occupancy for each season.

Another approach for future research, with regard to the temporal scale, could be to include camera trap data instead of sightings data. Camera traps have been used in multiple other studies regarding occupancy modelling (Calderón *et al.*, 2022; Van der Weyde *et al.*, 2018) and return unbiased data, whereas sightings data is dependable on observers. However, camera traps might not detect all individuals, as they are not able to scan over the area in the same way observers can. Camera traps have a fixed viewpoint. On the other hand, camera traps can provide information on the location of a study species at any time these species pass the camera sensors, possibly resulting in more frequent data on a cheetah's location compared to collecting sightings data with a limited amount of observers. This is something to take into account in further research concerning space use of species.

4.3 Livestock component

Similarly to my outcome on the livestock variable, previous research by Thuo *et al.* (2020) found no relationship between livestock predation by cheetahs and season in Kenya. This study was mainly diet focused, however, the outcome of the study by Thuo *et al.* (2020), that a similar amount of goat and sheep was present in cheetah diet in each season, could possibly indicate that livestock does not drive a seasonal difference in cheetahs' space use and that livestock predation does not differ seasonally. Previous research by Winterbach *et al.* (2015) has shown that cheetahs prefer wild prey over livestock, possibly as the risks of taking livestock outweigh the benefits. This means that even though the wild prey abundance is reduced out of migration, still a preference for wild prey is shown and livestock does not take up a substantial part in cheetahs' diet. A study by Khorozyan *et al.* (2015) showed that big cats show higher livestock predation when the wild prey has reached some kind of minimum threshold. It could be that in the season out of migration, the wild prey does not reach such a threshold yet and the cheetahs do not feel the need to predate on livestock as much. However, in this study I also did not find that cheetahs avoid livestock areas. Similarly, a study by Broekhuis *et al.* (2019) found that livestock did not affect the space use of cheetahs when moving. According to the study, livestock abundance only had an effect on whether cheetahs showed stationary bahaviour (e.g. feeding or resting).

According to previous research in Kenya, the livestock proportion of cheetahs' diet almost exclusively consisted of sheep and goats (Thuo *et al.*, 2020; Patterson *et al.*, 2004). In my model, all domesticated species found in the study area were taken into account. This means that apart from sheep and goats, cattle was also included in the livestock covariate in the model. As cattle is one of the most abundant livestock species in the dataset, the effect of livestock in the model was mostly based on the abundance of cattle. As cheetahs rarely prey on cattle (Patterson *et al.*, 2004), the livestock covariate might have underestimated the effect of livestock on cheetah space use over seasons, as goats and sheep were only a small component of the covariate. A study by Khorozyan *et al.* (2015) even shows that cheetah seem to avoid cattle. Cattle seems to be more of a disturbance for cheetahs, rather than prey species.

4.4 Limitations and recommendations

The best performing model, used in the analysis in this study, was found to be under-dispersed, indicating a lack of variation in the data. This is likely a result of the small sample size in this study, the lack of fitting covariates or a result of too many variables in the model (Lord & Guikema, 2012). The use of a small dataset can give an output which suggests that the sites are more similar to one another than they actually are. The under-dispersed model can be improved by adding several possibly driving covariates to the model. This could be other prey species found in cheetah's diet, such as impalas (*Aepyceros melampus*) or Grant's gazelles (*Gazella granti*; Broekhuis *et al.*, 2018), or other factors that might have an influence on their seasonal space use, such as human disturbance in or close to the wildlife areas, which has also been documented in other large carnivore species (Xiao *et al.*, 2022).

4.5 Application

This study provides insight in the consideration of various components when applying occupancy modelling, such as the spatial scale, the temporal scale and the separate sexes. Knowledge on the specific changes in cheetahs' space use over seasons is of high importance to create management to prevent the species from declining, as the species is already assessed as vulnerable by the Red List of the International Union for Conservation of Nature (IUCN; Durant *et al.*, 2022). Understanding the seasonal space use of cheetahs can improve conservation to protect the most important habitats for the cheetahs around the Maasai Mara, as over 70 percent of the cheetahs' range in Eastern Africa, and even globally, is outside protected areas (Durant *et al.*, 2017). A better knowledge on what areas are important for cheetahs and what factors are influencing the space use of cheetahs might aid future conservation by filling the knowledge gaps. Occupancy studies can act as useful indicators to highlight the most important sites for cheetahs and to assess the key drivers of their space use.

4.6 Conclusion

Large carnivores tend to spread in occupancy during migration as a response to high influx of wild prey. However, a deeper investigation needs to be done in order to find out which factors are driving the difference in occupancy per season, taking in consideration differences between sexes and the temporal and spatial scale.

Acknowledgements

For this study, I would like to thank my supervisor, Femke Broekhuis, for all the guidance and feedback she has given me throughout the process of this research. I am very grateful for it. I am also thankful for all peers who were kind enough to go through components of this work and provided me with useful feedback.

References

Arthur, S.M. & Del Vecchio, P.A. (2017). Effects of grizzly bear predation on muskoxen in northeastern Alaska. *Ursus, 28*(1). 81-91. https://doi.org/10.2192/URSU-D-16-00023.1

Atickem, A.; Simeneh, G.; Bekele, A.; Mekonnen, T.; Sillero-Zubiri, C.; Hill, R.A. & Stenseth, N.C. (2017). African wolf diet, predation on livestock and conflict in the Guassa mountains of Ethiopia. *African Juornal of Ecology, 55*(4). 632-639. https://doi.org/10.1111/aje.12399

Bissett, C. & Bernard, R.T.F. (2007). Habitat selection and feeding ecology of the cheetah (Acinonyx jubatus) in thicket vegetation: is the cheetah a savanna specialist? *Journal of Zoology, 271*(3). 310-317. https://doi.org/10.1111/j.1469-7998.2006.00217.x

Bissett, C.; Bernard, R.T.F. & Parker, D.M. (2012). The response of lions (Panthera leo) to changes in prey abundance on an enclosed reserve in South Africa. *Acta Theriologica, 57*(3). 225-231. https://doi.org/10.1007/s13364-011-0071-8

Broekhuis, F. & Gopalaswamy, A.M. (2016). Counting cats: Spatially explicit population estimates of cheetah (Acinonyx jubatus) using unstructured sampling data. *PLoS ONE, 11*(5). e0153875. https://doi.org/10.1371/journal.pone.0153875

Broekhuis, F.; Cushman, S.A. & Nicholas, B.E. (2017). Identification of human-carnivore conflict hotspots to prioritize mitigation efforts. *Ecology and Evolution, 7*(24). 10630-10639. https://doi.org/10.1002/ece3.3565

Broekhuis, F.; Thuo, D. & Hayward, M.W. (2018). Feeding ecology of cheetahs in the Maasai Mara, Kenya and the potential for intra- and interspecific competition. *Journal of Zoology, 304*(1). 65-72. https://doi.org/10.1111/jzo.12499

Broekhuis, F.; Madsen, E.K. & Klaassen, B. (2019). Predators and pastoralists: how anthropogenic pressures inside wildlife areas influence carnivore space use and movement behaviour. *Animal Conservation, 22*(4). 404-416. https://doi.org/10.1111/acv.12483

Broekhuis, F.; Elliot, N.B.; Keiwua, K.; Koinet, K.; Macdonald, D.W.; Mogensen, N.; Thuo, D. & Gopalaswamy, A.M. (2021). Resource pulses influence the spatio-temporal dynamics of a large carnivore population. *Ecography, 44*(3). 358-369. https://doi.org/10.1111/ecog.05154

Broekhuis, F.; Ngene, S.; Gopalaswamy, A.M.; Mwaura, A.; Dloniak, S.M.; Ngatia, D.K.; Tyrrell, P.D.; Yamane, Y. & Elliot, N.B. (2022). Predicting potential distributions of large carnivores in Kenya: An occupancy study to guide conservation. *Diversity and Distributions, 28*(7). 1445-1457. https://doi.org/10.1111/ddi.13554

Butt, B.; Shortridge, A. & WinklerPrins, A.M.G.A. (2009). Pastoral herd management, drought coping strategies, and cattle mobility in Southern Kenya. *Annals of the Association of American Geographers, 99*(2). 309-334. https://doi.org/10.1080/00045600802685895

Butt, B. (2010). Seasonal space-time dynamics of cattle behavior and mobility among Maasai pastoralists in semi-arid Kenya. *Journal of Arid Environments, 74*(3). 403-413. https://doi.org/10.1016/j.jaridenv.2009.09.025

Calderón, A.P.; Louvrier, J.; Araya-Gamboa, D.; Arroyo-Arce, S.; Barrantes-Núñez, M.; Carazo-Salazar, J.; Corrales-Gutiérrez, D.; Doncaster, C.P.; Foster, R.; García, M.J. & Garcia-Anleu, R. (2022). Occupancy models reveal potential of conservation prioritization for Central American jaguars. *Animal Conservation, 25*(5). 680-691. https://doi.org/10.1111/acv.12772

Caro, T.M. & Collins, D.A. (1987). Ecological characteristics of territories of male cheetahs (Acinonyx jubatus). *Journal of Zoology, 211*(1). 89-105. https://doi.org/10.1111/j.1469-7998.1987.tb07455.x

Dalerum, F.; Selby, L.O.K. & Pirk, C.W.W. (2020). Relationships Between Livestock Damages and Large Carnivore Densities in Sweden. *Frontiers in Ecology and Evolution, 7*. https://doi.org/10.3389/fevo.2019.00507

Dupont, B. (2022). Cheetah (Acinonyx jubatus) juvenile (CC BY-SA 2.0). *Flickr.*

Durant, S.M.; Caro, T.M.; Collins, D.A.; Alawi, R.M.; Fitzgibbon, C.D. (1988). Migration patterns of Thomson's gazelles and cheetahs on the Serengeti Plains. *African Journal of Ecology, 26*(4). 257-268. https://doi.org/10.1111/j.1365-2028.1988.tb00978.x

Durant, S.M.; Mitchell, N.; Groom, R.; Pettorelli, N.; Ipavec, A.; Jacobson, A.P.; Woodroffe, R.; Bohm, M.; Hunter, L.T.B.; Becker, M.S.; Broekhuis, F.; Bashir, S.; Andresen, L.; Aschenborn, O.; Beddiaf, M.; Belbachir, F.; Belbachir-Bazi, A.; Berbash, A.; Machado, I.B.D.; Breitenmoser, C.; Chege, M.; Cilliers, D.; Davies-Mostert, H.; Dickman, A.J.; Ezekiel, F.; Farhadinia, M.S.; Funston, P.; Henschel, P.; Horgan, J.; de Iongh, H.H.; Jowkar, H.; Klein, R.; Lindsey, P.A.; Marker, L.; Marnewick, K.; Melzheimer, J.; Merkle, J.; M'Soka, J.; Msuha, M.; O'Neill, H.; Parker, M.; Purchase, G.; Sahailou, S.; Saidu, Y.; Samna, A.; Schmidt-Kuntzel, A.; Selebatso, E.; Sogbohossou, E.A.; Soultan, A.; Stone, E.; van der Meer, E.; van Vuuren, R.; Wykstra, M. & Young-Overton K. (2017). The global decline of cheetah Acinonyx jubatus and what it means for conservation. *Proceedings of the National Academy of Sciences of the United States of America. 114*(3). 528-533. https://doi.org/10.1073/pnas.1611122114

Durant, S.M., Groom, R., Ipavec, A., Mitchell, N. & Khalatbari, L. (2022). *Acinonyx jubatus. The IUCN Red List of Threatened Species* 2022: e.T219A124366642. https://dx.doi.org/10.2305/IUCN.UK.2022-1.RLTS.T219A124366642.en.

Gigliotti, L.C.; Slotow, R.; Hunter, L.T.B.; Fattebert, J.; Sholto-Douglas, C. & Jachowski, D.S. (2020). Habitat complexity and lifetime predation risk influence mesopredator survival in a multi-predator system. *Scientific Reports, 10*(1). https://doi.org/10.1038/s41598-020-73318-3

Hilborn, A.; Pettorelli, N.; Caro, T.; Kelly, M.J.; Laurenson, M.K. & Durant, S. (2018). Cheetahs modify their prey handling behavior depending on risks from top predators. *Behavioural Ecology and Sociobiology, 72*(4). https://doi.org/10.1007/s00265-018-2481-y

Holdo, R.M.; Holt, R.D. & Fryxell, J.M. (2009). Opposting rainfall and plant nutritional gradients best explain the wildebeest migration in the Serengeti. *American Naturalist, 173*(4). 431-445. https://doi.org/10.1086/597229

Hongo, S.; Nakashima, Y.; Akomo-Okoue, E.F. & Mindonga-Nguelet, F.L. (2018). Seasonal Change in Diet and Habitat Use in Wild Mandrills (Mandrillus sphinx). *International Journal of Primatology, 39*(1). 27-48. https://doi.org/10.1007/s10764-017-0007-5

Fiske, I. & Chandler, R. (2011). unmarked: An R Package for Fitting Hierarchical Models of Wildlife Occurrence and Abundance. *Journal of Statistical Software, 43*(10). 1-23. https://www.jstatsoft.org/v43/i10/

Igor, K.; Arash, G.; Mahmood, S. & Matthias, W. (2015). Big cats kill more livestock when wild prey reaches a minimum threshold. *Biological Conservation, 192*. 268-275. https://doi.org/10.1016/j.biocon.2015.09.031

IUCN SSC. 2007a. Regional conservation strategy for the cheetah and African wild dog in Eastern Africa. IUCN Species Survival Commission, Gland, Switzerland.

Kellner, K.F.; Smith, A.D.; Royle, J.A.; Kery, M.; Belant, J.L. & Chandler, R.B. (2023). The unmarked R package: Twelve years of advances in occurrence and abundance modelling in ecology. *Methods in Ecology and Evolution, 14*(6). 1408-1415. https://doi.org/10.1111/2041-210X.14123

Khorozyan, I.; Ghoddousi, A.; Soofi, M. & Waltert, M. (2015). Big cats kill more livestock when wild prey reaches a minimum threshold. *Biological Conservation, 192.* 268-275. https://doi.org/10.1016/j.biocon.2015.09.031

King, T.W.; Vynne, C.; Miller, D.; Fisher, S.; Fitkin, S.; Rohrer, J.; Ransom, J.I. & Thornton, D.H. (2021). The influence of spatial and temporal scale on the relative importance of biotic vs. abiotic factors for species distributions. *Diversity and Distributions, 27*(2). 327-343. https://doi.org/10.1111/ddi.13182

Kissui, B.M. (2008). Livestock Predation by lions, leopards, spotted hyenas, and their vulnerability to retaliatory killing in the Maasai steppe, Tanzania. *Animal Conservation, 11*. 422-432. https://doi.org/10.1111/j.1469-1795.2008.00199.x

Kittle, M.; Bukombe, J.K.; Sinclair, R.E.; Mduma, S.A.R. & Fryxell, J.M. (2016). Landscape-level movement patterns by lions in western Serengeti: comparing the influence of inter-specific competitors, habitat attributes and prey availability. Movement Ecology, 4(17). https://doi.org/10.1186/s40462-016-0082-9

Klaassen, B. & Broekhuis, F. (2018). Living on the edge: Multiscale habitat selection by cheetahs in a human-wildlife landscape. *Ecology and Evolution, 8*(15). 7611-7623. https://doi.org/10.1002/ece3.4269

Kleiven, E.F.; Barraquand, F.; Gimenez, O.; Henden, J.A.; Ims, R.A.; Soininen, E.M. & Yoccoz, N.G. (2023). A Dynamic Occupancy Model for Interacting Species with Two Spatial Scales. *Journal of Agricultural, Biological, and Environmental Statistics, 28*(3). 466-482. https://doi.org/10.1007/s13253-023-00533-6

Lakshminarayanan, N.; Karanth, K.K.; Goswami, V.R.; Vaidyanathan, S. & Karanth, K.U. (2016). Determinants of dry season habitat use by Asian elephants in the Western Ghats of India. *Journal of Zoology, 298*(3). 169-177. https://doi.org/10.1111/jzo.12298

Lord, D. & Guikema, S.D. (2012). The Conway-Maxwell-Poisson model for analyzing crash data. *Applied Stochastic Models in Business and Industry, 28*(2). 122-127. https://doi.org/10.1002/asmb.937

MacKenzie, D.I.; Nichols, J.D.; Lachman, G.B.; Droege, S.; Royle, J.A. & Langtimm, C.A. (2002). Estimating site occupancy rates when detection probabilities are less than one. *Ecology, 83*(8). 2248-2255. https://doi.org/10.1890/0012-9658(2002)083[2248:ESORWD]2.0.CO;2

MacKenzie, D.I.; Nichols, J.D.; Hines, J.E.; Knutson, M.G. & Franklin, A.B. (2003). Estimating site occupancy, colonization, and local extinction when a species is detected imperfectly. *Ecology, 84*(8). 2200-2207. https://doi.org/10.1890/02-3090

Midlane, N.; O'Riain, M.J.; Balme, G.A.; Robinson, H.S. & Hunter, L.T.B. (2014). On tracks: A spoor-based occupancy survey of lion Panthera leo distribution in Kafue National Park, Zambia. *Biological Conservation, 172*. 101-108. https://doi.org/10.1016/j.biocon.2014.02.006

Mills, M.G.L.; Broomhall, L.S. & Du Toit, J.T. (2004). Cheetah Acinonyx jubatus feeding ecology in the Kruger National Park and a comparison across African savanna habitats: Is the cheetah only a successful hunter on open grassland plains? *Wildlife Biology, 10*(3). 177-186. https://doi.org/10.2981/wlb.2004.024

Mkonyi, F.J.; Estes, A.B.; Lichtenfeld, L.L. & Durant, S.M. (2018). Large carnivore distribution in relationship to environmental and anthropogenic factors in a multiple-use landscape of Northern Tanzania. *African Journal of Ecology, 56*(4). 972-983. https://doi.org/10.1111/aje.12528

Morato, R.G.; Connette, G.M.; Stabach, J.A.; De Paula, R.C.; Ferraz, K.M.P.M.; Kantek, D.L.Z.; Miyazaki, S.S.; Pereira, T.D.C.; Silva, L.C.; Paviolo, A.; De Angelo, C. & Di Bitetti, M.S. (2018). Resource selection in an apex predator and variation in response to local landscape characteristics. *Biological Conservation, 228*. 233-240. https://doi.org/10.1016/j.biocon.2018.10.022

Ogutu, J.O.; Plepho, H.P.; Doublin, H.T.; Bhola, N. & Reld, R.S. (2008). Rainfall influences on ungulate population abundance in the Mara-Serengeti ecosystem. *Journal of Animal Ecology, 77*. 814-829. https://doi.org/10.1111/j.1365-2656.2008.01392.x

Ogutu, J.O.; Piepho, H.P.; Said, M.Y.; Ojwang, G.O.; Njino, L.W.; Kifugo, S.C. & Wargute, P.W. (2016). Extreme wildlife declines and concurrent increase in livestock numbers in Kenya: What are the causes? *PLoS ONE, 11*(9). https://doi.org/10.1371/journal.pone.0163249

Oindo, B.O.; Skidmore, A.K. & De Salvo, P. (2003). Mapping habitat and biological diversity in the Maasai Mara ecosystem. *International Journal of Remote Sensing, 24*(5). 1053-1069. https://doi.org/10.1080.01431160210144552

Patterson, B.D.; Kasiki, S.M.; Selempo, E. & Kays, R.W. (2004). Livestock predation by lions (Panthera leo) and other carnivores on ranches neighboring Tsavo National Park, Kenya. *Biological Conservation, 119*(4). 507-516. https://doi.org/10.1016/j.biocon.2004.01.013

QGIS Development Team (2015) QGIS Geographic Information System. Open Source Geospatial Foundation Project http://qgis.osgeo.org.

QGIS Development Team (2021) QGIS Geographic Information System. Open Source Geospatial Foundation Project http://qgis.osgeo.org.

R Development Core Team (2016). R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria.

R Development Core Team (2023). R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria.

Rota, C.T.; Ferreira, M.A.R.; Kays, R.W.; Forrester, T.D.; Kalies, E.L.; McShea, W.J.; Parsons, A.W. & Millspaugh, J.J. (2016). A multispecies occupancy model for two or more interacting species. *Methods in Ecology and Evolution, 7*(10). 1164-1173. https://doi.org/10.1111/2041-210X.12587

Sargent, R.; Deere, N.J.; McGowan, P.J.K.; Bunnefeld, N. & Pfeifer, M. (2022). Room to roam for African lions Panthera leo: a review of the key drivers of lion habitat use and implications for conservation. *Mammal Review, 52*(1). 39-51. https://doi.org/10.1111/mam.12262

Schooler, S.L.; Finnegan, S.P.; Fowler, N.L.; Kellner, K.F.; Lutto, A.L.; Parchizadeh, J.; Van den Bosch, M.; Zubiria Perez, A.; Masinde, L.M.; Mwampeta, S.B.; Boone, H.M.; Gantchoff, M.G.; Hill, J.E.; Kautz, T.M.; Wehr, N.H.; Fyumagwa, R. & Belant, J.L. (2022). Factors influencing lion movements and habitat use in the western Serengeti ecosystem, Tanzania. *Scientific Reports, 12*(1). https://doi.org/10.1038/s41598-022-22053-y

Tambling, C.J.; Wilson, J.W.; Bradford, P. & Scantlebury, M. (2014). Fine-scale differences in predicted and observed cheetah diet: does sexual dimorphism matter? *South African Journal of Wildlife Research, 44*(1). 90-94. https://doi.org/10.3957/056.044.0109

Thuo, D.F.; Broekhuis, F.; Furlan, E.; Bertola, L.D.; Kamau, J. & Gleeson, D.M. (2020). An insight into the prey spectra and livestock predation by cheetahs in Kenya using faecal DNA metabarcoding. *Zoology, 143*. https://doi.org/10.1016/j.zool.2020.125853

Van der Weyde, L.K.; Mbisana, C. & Klein, R. (2018). Multi-species occupancy modelling of a carnivore guild in wildlife management areas in the Kalahari. *Biological Conservation, 220*. 21-28. https://doi.org/10.1016/j.biocon.2018.01.033

Viana, D.S. & Chase, J.M. (2019). Spatial scale modulates the inference of metacommunity assembly processes. *Ecology, 100*(2). https://doi.org/10.1002/ecy.2576

Vettorazzi, M.; Mogensen, N.; Kaelo, B & Broekhuis, F. (2022). Understanding the effects of seasonal variation in prey availability on prey switching by large carnivores. *Journal of Zoology, 318*(3). 218-227. https://doi.org/10.1111/jzo.13013

Welch, R.J.; Bissett, C.; Perry, T.W. & Parker, D.M. (2015). Somewhere to hide: Home range and habitat selection of cheetahs in an arid, enclosed system. *Journal of Arid Environments, 114.* 91-99. https://doi.org/10.1016/j.jaridenv.2014.11.012

Winterbach, H.E.K.; Winterbach, C.W.; Boast, L.K.; Klein, R. & Somers, M.J. (2015). Relative availability of natural prey versus livestock predicts landscape suitability for cheetahs Acinonyx jubatus in Botswana. *PeerJ, 2015*(7). https://doi.org/10.7717/peerj.1033

Xiao, C.; Bai, D.; Lambert, J.P.; Li, Y.; Cering, L.; Gong, Z.; Riordan, P. & Shi, K. (2022). How Snow Leopards Share the Same Landscape with Tibetan Agro-pastoral Communities in the Chinese Himalayas. *Journal of Resources and Ecology, 13*(3). 483-500. https://doi.org/10.5814/j.issn.1674-764x.2022.03.013

Zanón Martínez, J.I.; Iranzo, E.C.; Travaini, A.; McNitt, D.C.; Mansilla, A.P.; Llanos, R. & Kelly, M.J. (2023). Puma density, habitat use, and activity patterns across a mosaic landscape of ranches, game reserves, and a protected area in central Argentina. *European Journal of Wildlife Research, 69*(5). https://doi.org/10.1007/s10344-023-01717-8