

**Determining multi-species site use outside the protected areas of the Maasai Mara,
Kenya, using false positive site-occupancy modeling**

Emily K. Madsen^{1,2*} and Femke Broekhuis^{3,4}

¹ Royal Veterinary College, 4 Royal College St, Kings Cross, London, NW1 0TU, United Kingdom

² The Zoological Society of London, Institute of Zoology, Outer Circle, Regents Park, London, NW1 4RY, United Kingdom

³ Cheetah Project, Kenya Wildlife Trust, P.O. Box 86, 00502 Karen, Nairobi, Kenya

⁴ Wildlife Conservation Research Unit, Department of Zoology, University of Oxford, Recanati-Kaplan Centre, Tubney House Abingdon Road, Tubney, Oxfordshire OX13 5QL, United Kingdom

* Corresponding author

E-mail: emadsen6@rvc.ac.uk

Word count: 6640

Abstract

Protected areas are the basis for many conservation plans for wildlife. However, they are rarely of an adequate size for the long term survival of populations of large, wide-roaming mammals. In the Maasai Mara, Kenya, communally owned wildlife conservancies have been developed to expand the area available for wildlife. As these continue to develop it is important to ensure that the areas chosen are beneficial to wildlife. Using presence data on cheetah (*Acinonyx jubatus*), elephant (*Loxodonta africana*), spotted hyaena (*Crocuta crocuta*), leopard (*Panthera pardus*), lion (*P. leo*) and wild dog (*Lycaon pictus*), collected through interviews with people living outside the protected areas (n=648), we identify key wildlife areas using false positive site-occupancy modelling. The probabilities of site use were first determined per species based on habitat, protected area distance, river distance and human presence and these were then combined to create a species richness map to highlight key wildlife areas. All six species, except hyaena, showed a preference for a certain habitat type and all avoided human presence. Leopard, elephant, lion and wild dog preferred sites closer to rivers. Hyaena showed minimal influence by distance from protected areas but the other five species all selected for sites closer to the protected areas. The resulting species richness map highlights important areas for conservation efforts, including the expansion of wildlife areas and areas where human development, such as a newly tarmacked road, could have an impact on wildlife.

Keywords: Carnivores, false positive, interview data, Maasai Mara, mapping, occupancy, protected areas, wildlife distributions

Introduction

Protected areas are becoming the basis for the majority of conservation efforts. However, they often are not large enough to maintain sustainable populations of many species (Stokes et al., 2010; Okello et al., 2016). Approximately 15.4% of the world's terrestrial area is now formally protected and in Kenya 8% of the land is protected as either a national park or reserve (Western et al., 2009). Nonetheless, 65-70% of the country's wildlife resides in unprotected areas where they are under threat by humans (Western et al., 2009; Stolton et al., 2014) and so there is a desire to protect more land for wildlife (Kenyan Wildlife and Conservation Act, 2013 (No. 47 of 2013)). The Maasai Mara in the South West of Kenya, for example, is renowned for its annual migration of wildebeest (*Connochaetes taurinus*) and high densities of predators (Broekhuis & Gopalaswamy, 2016; Elliot & Gopalaswamy, 2017) but, like many landscapes around the world, it is under increasing anthropogenic pressure. In the last few decades areas outside the protected areas have seen a rapid increase in human population growth and fencing of private land (Lamprey & Reid, 2004; Løvschal et al., 2017) which has resulted in wildlife populations decreasing by up to 75% in the last century (Ogutu et al., 2011). The Maasai Mara National Reserve (MMNR) covers 1,503km² and in the last 25 years areas around the MMNR have been put aside for wildlife to try to address these population declines (Jandreau & Berkes, 2016). These areas are classified as "Community Wildlife Conservancies" by the IUCN and do not have the same status as the MMNR but are nonetheless recognised as being beneficial to wildlife (Stolton et al., 2014). The conservancies are areas where the landowners limit their resource use whilst receiving an income from tourist operators who pay for exclusive access (Jandreau & Berkes, 2016). The development of conservancies has so far added roughly 1000km² of designated wildlife area to the MMNR with the plan to increase this further (MMWCA, 2015). It is therefore important to ensure that the areas chosen will actually be beneficial to wildlife conservation. However, land protection schemes can be very costly which is why planning needs to be based upon reliable information, from evidence-based research, to ensure cost effectiveness (Zeller et al., 2011).

Land protection schemes are often based on species' occurrence because presence/absence data are easier and cheaper to collect than demographic data such as densities or whole population counts (Gu & Swihart, 2004). Information on wildlife presence can be collected through local people, as they often hold good knowledge of their local ecosystem and the wildlife that inhabits it, that can provide insights into the distribution of wildlife (Turvey et al., 2015). Interview surveys can be a useful method of collecting this information due to their cost-effectiveness and relative logistic simplicity (Turvey et al., 2015; Petracca et al., 2017). However, as is the case with all types of observational data, the use of untrained individuals increases the chance that false positive detections will occur through, for example, misidentification or false reporting, resulting in an overestimation of occupancy (Royle & Link, 2006; Petracca et al., 2017). This can be accounted for by focussing on easily recognisable species (Miller et al., 2011) and by using models which account for false positives (Royle & Link, 2006).

Another factor that needs to be taken into account is detection probability. For example, presence/absence data may be biased towards habitats where there is a higher chance that an animal is detected, such as open plains compared to woodlands where detection might be hindered. If this is not accounted for then the outputs might not correctly predict the areas that are most suitable for wildlife (Pulliam, 1988). The detection probability may also be influenced by the amount of time that a person spends outside which is likely to vary with occupation (Turvey et al., 2015). These variations can be difficult to quantify for analysis and some studies chose to use the proportion of the year or another continuous covariate to account for effort (Zeller et al., 2011), however this is not possible if the interviewee is constantly resident in their area and so categorical variables may be used. Additionally, assuming that non-detection equates to absence could result in a negative bias in occupancy estimates (MacKenzie et al., 2002; MacKenzie et al., 2003). Imperfect detection can be accounted for by repeating surveys in each site which enables the calculation of detection probability using the detection history of each site (MacKenzie et al., 2002). Failure to account for imperfect detection can lead to unreliable results and so lead to ill-informed

conservation decisions (MacKenzie et al., 2002; MacKenzie et al., 2004). Both detection probability and imperfect detection can be accounted for using site-occupancy modelling, a well-established method for using presence/absence data to determine wildlife distributions which can be an alternative to density estimations (Pillay et al., 2011). These models have been expanded to account for false-positives (Royle & Link, 2006) and when false positives are accounted for, interview data can provide robust results on species presence and distribution (Petracca et al., 2017).

Here we use interview data and false-positive occupancy modelling to identify areas of high wildlife use outside the protected areas of the Maasai Mara, Kenya, with the main aim being to highlight conservation priority locations for the potential expansion of protected areas. Basing management decisions on a single species may be unreliable because different species show variation in behavioural plasticity when faced with threats (Woodroffe, 2000) so we used a multi-species approach focused on six large mammals: cheetah (*Acinonyx jubatus*), elephant (*Loxodonta africana*), spotted hyaena (*Crocuta crocuta*), leopard (*Panthera pardus*), lion (*P. leo*) and wild dog (*Lycaon pictus*). Carnivores were the main focus because they can have wide-ranging, keystone effects on their ecosystem and the protection of intact guilds of carnivores is of particular importance because of their ecological effects (Ripple et al., 2014; Wolf & Ripple, 2017). They are also sensitive to human disturbance (Woodroffe, 2000), which is significant when setting aside areas for protection in a human-dominated landscape like the Maasai Mara. As the species chosen have different ecological requirements we hypothesise that their distributions will vary. Based on key landscape variables, which include habitat, human presence, distance to protected areas and distance to rivers, we have summarised our predictions in Table 1.

Study area

The study was conducted in the Maasai Mara (centred at 1°S, 35°E; elevation c. 1700 m) in southwestern Kenya. Data were collected in sites around the Maasai Mara National Reserve and the adjacent wildlife conservancies which will hereafter be referred to as the protected areas (Fig. 1). To

the south, the Maasai Mara National Reserve borders the Serengeti National Park in Tanzania, to the north and west it borders intensive agricultural land and the east is largely pastoralist settlement (Fig. 1). There are no physical barriers between the protected areas and the surrounding community areas, allowing for free movement of animals.

Methods

Data collection

Data on the frequency of sightings of cheetah, elephant, spotted hyaena, leopard, lion and wild dog were collected through semi-structured interviews that were conducted in June and July 2015. Ten Maasai men from the community, who had previous experience in conducting questionnaire-based interviews, were employed to conduct the survey. In total, 820 interviews were conducted and, in accordance with Maasai customs, the most senior male of each household was interviewed (see Broekhuis et al., 2017 for details). Data on individuals were kept confidential and collected in line with Zoological Society of London's (ZSL) guidelines and methods were approved by the ZSL Ethical Committee.

A respondent's occupation could influence the amount of time spent outdoors, which in turn could affect the possibility of seeing wildlife if it were present. Therefore, at the start of each interview the respondents were asked which of the following they considered to be their main occupation; agriculturist, pastoralist, tourism, business or other. For the analysis, agriculturist, business and other were grouped as "other" to assist in model convergence as the proportions were low compared to tourism and pastoralist. To assess the respondent's ability to identify the species of interest they were presented with photographs of cheetah, elephant, spotted hyaena, leopard, lion and wild dog which they were asked to identify. Only data from respondents who correctly identified the species were included in the analysis. The respondents were then asked how frequently they saw each of these species in the area that their household was in; yearly, monthly, weekly, daily or never. Their interpretation of their area may have some variability, however, it would not be larger than 5x5km (Michael Kaelo, pers. comm.).

Environmental variables

Eight environmental variables in four different categories, were chosen based on previous findings (Table 1) and extracted per site but, depending on the model selection outputs (see '*Site occupancy modelling*'), only one variable per category was used for each species to assist in model convergence (Petracca et al., 2017).

Human presence - four different variables were used to quantify human presence: the average distance to the nearest human development, the average human density, the sum of the human density and the proportion of fenced areas, which we included in this category as it was correlated to human presence. Anthropogenic features such as clusters of buildings and livestock enclosures were digitised using QGIS (QGIS Development Team 2017) with the OpenLayers plugin for both Google Earth and Bing maps. The Euclidean distance to each anthropogenic feature was calculated and averaged per site. The density of the anthropogenic features was calculated by drawing polygons around each human development, to reflect its size, which were then converted to points. Using the *point density* function in ArcGIS 10.4.1 (Environmental Systems Research Institute Inc., 2014) the density of human development was calculated and then averaged and summed per site. The proportion of the area that was fenced per site was calculated using fence data from 2015 available from Løvschal et al. (2017).

Habitat type – The habitat map included three habitat types; open, semi-closed and closed. Open habitat represented mainly grasslands, semi-closed included Acacia woodland and croton (*Croton dichogamus*) bushes and closed was predominantly riparian (see Broekhuis et al., 2017 for details). Closed habitat was merged with semi-closed habitats as the proportions of closed were relatively low and using semi-closed habitat to predict occupancy then the probability would increase in both open and closed habitat. The proportions of open and semi-closed habitat were then calculated for each site.

Protected areas and rivers - The Euclidean distances to the protected areas and rivers were calculated and averaged per site.

All the spatial calculations were performed in ArcGIS 10.4.1 (Environmental Systems Research Institute Inc., 2014) and all the environmental variables, except those that were proportions, were standardized using a z-score transformation with a mean of 0 and a standard deviation of 1.

Site-occupancy modelling

We were interested in species' distributions outside the protected areas so only interviews that were conducted outside the protected areas were analysed using a single-season occupancy model using the package *unmarked* (Fiske & Chandler, 2011) in R 3.4.0 (R Development Core Team, 2016). The study area was divided into 5 x 5 km sites as this was believed to be fine-scale enough to provide useful information for planning future conservancies and corridors (Fig. 1). The 5 x 5 km sites were smaller than the average home ranges of the species being assessed which violates the assumption of closure, therefore; psi (ψ) was interpreted as the "probability of site use" rather than the "probability of occupancy" (Zeller et al., 2011; Alexander et al., 2016). Other assumptions of occupancy modelling, such as no false positives and no modelled heterogeneity, are accounted for in our models. Each interview within a site was treated as a repeat survey and the number per site was randomly reduced to a maximum of 10 to minimise the variance to aid in model convergence (Petracca et al., 2017). The potential for false positives was accounted for in the model by introducing a binary variable designating "1" as equal to, or over, the mean number of surveys (6) and "0" as less than the mean, because the probability is expected to increase with the number of surveys per site (Royle & Link, 2006; Petracca et al., 2017). The following model was used:

$$L(\mathbf{p}, \psi | \mathbf{y}) \propto \prod_{i=1}^R \{ [p_{11}^{y_i} (1 - p_{11})^{T-y_i}] \psi + [p_{10}^{y_i} (1 - p_{10}) a^{T-y_i}] (1 - \psi) \}$$

Where p_{10} = false detection probability, p_{11} = true detection probability, R = number of sites, y_i = number of detections at site i and T = total survey number at site i .

To create detection histories for each site, daily and weekly sightings were considered a presence (1) and all other sightings an absence (0), however, for wild dogs, monthly sightings were also used as a presence as wild dogs are an uncommon occurrence. This distinction was used as the aim was to identify the areas of the highest levels of site use, daily and weekly sightings likely indicate an animal which incorporates the site as part of its home range whereas less frequent sightings indicate that the animals are likely transients.

A respondent's occupation, the proportion of open habitat or a combination of the two were believed to influence the detection probability and account for heterogeneity, so each model was run separately and the variable(s) in the model with the lowest Akaike Information Criterion (AIC) (Burnham & Anderson, 2002) were used in the subsequent analysis. Within the human presence and habitat categories, univariate models were run and the AIC values were used to determine which variable within each category best predicted the site use per species. Pearson's correlation tests were run on the variables selected in the univariate analysis stage with a threshold of $|r| > 0.6$ indicating correlation (Dormann et al., 2013). Uncorrelated variables were then used in the multivariate models which included the top variables in the human presence and habitat categories and the distances to the protected areas and rivers. The *a-priori* candidate models were ranked using AIC and the relative support was assessed using the ΔAIC and AIC weights. If the top model AIC weight was < 0.9 then the probability of site use was averaged using a weighted method for all the models with $\Delta AIC < 2$ (Burnham & Anderson, 2002). Models and model comparison statistics can be found in the Supplementary Material. The results from the top models were used to predict the probability of site use (ψ) for sites without interviews using the following equation in excel:

$$\psi = \frac{\exp[\alpha + (\beta * D_1) + (\beta * D_2) \dots (\beta * D_5)]}{1 + \exp[\alpha + (\beta * D_1) + (\beta * D_2) \dots (\beta * D_5)]}$$

Where D_{1-5} = site use covariates and β_{1-5} = estimated coefficients.

The averaged probabilities of site use were individually mapped for each species and then summed to generate a species richness map using ArcGIS 10.4.1 (Environmental Systems Research Institute Inc., 2014).

Results

In total, 648 interviews were conducted outside the protected areas in 67 of 139 sites and the number of interviews per site ranged from 1-10 (Fig. 1). Only those data where species were correctly identified were used, resulting in different samples sizes; cheetah N=584, hyaena N=642, leopard N=577, wild dog N=598, lion N=648 and elephant N=648. The Pearson's correlation tests indicated that none of the variables in the different univariate analysis groups were correlated with $|r| < 0.6$. The false positive model did not converge for hyaena so the simple single-season model was used instead. For all the other species the false positive model was used. Additionally, out of the two models with a $\Delta AIC < 2$ for hyaena, the second model did not converge so only the top model was used for prediction of site use. For all the species the detection probability coefficients improved the predictive ability of the model from the null. The proportion of open habitat had the best predictive ability for the probabilities of detecting cheetah, lion and wild dog. For lion the probability of detection increased with proportion of open habitat, however, for wild dog and cheetah the probability of detection decreased but the effect was minimal (Table 2). For elephant and leopard the combination of the respondents' occupation and the proportion of open habitat had the best fit for the detection probabilities. The proportion of open habitat also increased the probability of detecting elephants but was less important for leopard with confidence intervals crossing zero. For hyaena, only the occupation of the respondent was in the final model.

All species, except hyaena, had a habitat parameter in their final occupancy models (Table 3). In the univariate habitat covariate selection, lion and wild dog probabilities of site use were best

predicted by the proportion of semi-closed habitat with both showing a positive relationship as predicted (Table 1). Site use by cheetah, elephant and leopard, on the other hand, were all best predicted by the proportion of open habitat. Cheetah probability of site use increased with proportion of open habitat which was expected (Table 1) whereas the probability of site use for both elephant and leopard decreased with the proportion of open habitat. All six species were affected by human presence (Table 2). For cheetah, lion, leopard and hyaena the human presence covariate with the best fit was the mean human distance in the univariate analysis, with all showing a preference for sites further away from human presence which was expected for all except leopard (Table 1). However, for both lion and leopard this effect was minimal. The probability of site use for both elephant and wild dog decreased with an increased proportion of fences which had the best predictive value of the human presence covariates. All six species contained the mean distance to protected area in their top models with all, except hyaena, decreasing in probability of site use with distance from protected area, although cheetah, lion and wild dog all have confidence interval which cross zero (Table 2). Hyaena and wild dog's confidence intervals also indicate that the coefficients may be zero but showed relatively even proportions in both directions. Elephant, leopard, lion and wild dog all had the distance to rivers in their top models with all four showing a decrease in probability of site use with increased distance (Table 2) and this response was predicted for these species (Table 1).

The predicted values of the probability of site use for each of the species were mapped to show possible distribution (Fig. 2). Both elephant (average probability of site use of 0.553) and hyaena (0.910) had a wide distribution in the unprotected areas whereas leopards had the most restricted distribution (0.130). Wild dog distribution (0.176) appears to be divided into two distinct areas, one in the south east and one in the north, whereas lions (0.547) and cheetahs (0.598) are present around the boundaries of the protected areas. These species-specific maps were then summed to generate a species richness map (Fig. 3) which highlights an important wildlife area to the East of the Maasai Mara National Reserve.

Discussion

The main aim of this study was to identify areas outside the protected areas with the highest level of use by cheetah, elephant, spotted hyaena, leopard, lion and wild dog, to determine key wildlife areas for future land protection schemes. We also aimed to identify the main covariates which influenced site use for each species to aid in management decisions to better ensure the survival of these species. Site use varied greatly between species, possibly due to their differences in behavioural patterns and resource requirements. The distance from humans came out as the most informative of the human presence covariates for all the species, indicating that they avoid any human presence no matter how high the density. Additionally, the two human density covariates only accounted for the human presence within the site whereas the mean human distance also takes into account the surrounding sites. This could indicate that these species take into account the human presence on a wider scale and not just in their vicinity. The avoidance of humans has been shown in multiple large carnivore species (e.g. Schuette et al., 2013), possibly due to the negative interactions associated with people as a result of human-carnivore conflict (Loveridge et al., 2017). Leopards might be the exception, as they have been found to persist in many human-dominated landscapes (Athreya et al., 2013). This is not reflected in their distribution in this study which could be the result of the high levels of grazing and agriculture reducing the amount of suitable habitat for them in unprotected areas or because they are difficult to detect. For elephants and wild dogs, the proportion of fences negatively influenced presence, although the effect was marginal. Previous studies have shown that, even though elephants have the ability to break through fences, fences can have a strong negative impact on elephant movement (Thouless & Sakwa, 1995; Loarie et al., 2009). The continued increase in fencing around the Mara (Løvschal et al., 2017) could therefore prove to be very problematic for elephant movement. In the Mara, wild dogs are rarely reported within the protected areas but they are found in human-dominated areas. The results indicate that wild dog presence is more likely to be influenced by fences than by human presence, possibly because fences restrict their wide-ranging behaviour. Although hyaenas strongly avoided human presence, they still

had the widest distribution outside of the protected areas. Other studies have shown that, rather than avoiding areas of high human and livestock presence, that they change their activity patterns and this behavioural plasticity could explain their distribution (Kolowski et al., 2007; Kolowski & Holekamp, 2009).

Habitat covariates differed markedly between the six species which could be related to resource requirements and, for carnivores, it could reflect their different hunting strategies. Cheetah presence was influenced by the proportion of open habitat, which aligns with previous findings that cheetah use grasslands, possibly to increase their hunting success, as they are cursorial hunters (Bissett & Bernard, 2007; Broekhuis et al., 2013). Both lions and leopards, which are stalk and ambush hunters, preferred semi-closed habitat which is similar to findings from other areas (Hopcraft et al., 2005; Balme et al., 2007). In addition, for leopards the presence of trees in the semi-closed habitat provide opportunities to cache food to reduce kleptoparasitism (Balme et al., 2007; Balme et al., 2017a). Similarly, wild dogs selected for semi-closed habitat, possibly to minimise detection and reduce the risk of kleptoparasitism (Creel & Creel, 1998; Carbone et al., 2005). Other studies have shown that hyaenas select for semi-closed habitat with an avoidance of open areas (Kolowski & Holekamp, 2009). This is not reflected in this study but this could be due to habitat selection not being strong enough at the scale of this study. Elephants preferred semi-closed over open habitat which is likely related to the availability of browse or could be a result of a desire to minimise detection and avoid livestock which will often be grazing in open habitat (Galanti et al., 2006).

Site use for all species, except hyaena, decreased with increased distance from the protected areas. This is not surprising as various studies have shown that species, such as elephant, prefer to use areas in, or close, to the protected areas (Douglas-Hamilton et al., 2005; Galanti et al., 2006). For hyaenas, on the other hand, this might not be the case as they are able to persist in human-dominated areas outside the protected areas.

Rivers influenced the presence of lions, leopards, wild dogs and elephants and could be related to the dense vegetation found around rivers. Leopards, wild dogs and lions have been shown to select for similar habitats, including rivers, as they provide a cool environment during the day, denning opportunities for females with offspring and for increased hunting opportunities (Spong, 2002). De Knecht et al. (2011) theorised that, on a fine scale, elephants do not always need to be close to a water source, as long as there is one within a day's walking distance. Therefore, the availability of water is unlikely to be a limiting factor in the Mara as water sources are regularly distributed. It is therefore likely that the selection for rivers is instead a reflection of the type habitat that is found around rivers.

The individual species distribution maps are supported by both sighting and collar data from the different species, in particular cheetahs (Klaassen, 2017) and wild dogs (Masenga et al., 2016). Lions have a much wider distribution than leopards, despite these species selecting for similar habitat (Balme et al., 2017b) and this likely reflects the higher densities at which lions occur in the Mara (Elliot & Gopalaswamy, 2017). Cheetahs and lions were found in similar areas and, while lions pose a direct risk to cheetahs, these species can co-exist through fine-scale avoidance behaviour (Broekhuis et al., 2013). Wild dogs, on the other hand, had an inverse distribution to that of lions which is similar to findings from Botswana (Cozzi, 2012) and South Africa (Darnell et al., 2014). Such avoidance behaviour will affect the patterns of co-occurrence (MacKenzie et al., 2004). This illustrates the importance of taking a multi-species, rather than a single species, approach to management as the expansion of the protected areas could increase lion presence and numbers which could have a negative impact on the population of wild dogs in the Mara. Potential species interactions, therefore, need to be taken into account when deciding on management practices and may require further investigation.

The combined species richness map shows that site use is highest east and north of the protected areas. Compared to other areas with a similar distance to protected areas, the area north

of Naboisho and East of Olare-Motorogi conservancies (also known as the Pardamat Plains) had a low level of site use for all the species. This is likely a result of the very open habitat providing little cover for wildlife. The area south of Naboisho and Ol Kinyei conservancies appears to have the highest site use for all species. This could prove problematic as the Sekanani road, which passes through this area, is now in the process of being tarmacked which could have negative consequences for the dispersal of these species, and others, unless adequately mitigated.

The covariates used in this study were on a relatively broad scale and it is possible that there are others acting on a finer scale affecting the wildlife distribution. For example, elephants have been shown to have very seasonal habitat preferences and more fine scale preferences when it comes to plant composition (Galanti et al., 2006; Shannon et al., 2006). Additionally, gradient and elevation have been shown to influence leopard site use which was not taken into account in this study (Balme et al., 2017b). There could also be other factors which affect the respondents' probability of seeing a species; not all pastoralists will spend equal amounts of time with their livestock. One potential limitation of this study is that it was difficult to ensure that the interviewees only reported on their site and did not include sightings that may have happened in other areas. However, the false positive model should have accounted for the potential for a small number of interviewees reporting on a wider area than intended.

The interview methodology provides an opportunity to rapidly assess the distribution of wildlife in unprotected areas and has the potential to be developed into a long-term monitoring program to assess changes over time. The use of the false positive model increases the robustness of the results derived from untrained individuals (Petracca et al., 2017). The resultant covariates in the models agree on the whole with published literature and expert opinion. The combined species richness map highlights areas of the highest level of use by all the species and indicated that it is the areas to the east, between the main body of protected areas and the outer conservancies, which have the highest level of use. These areas are recommended for future conservation planning

priorities which could include the expansion of current conservancies and the creation of new conservancies and wildlife corridors to ensure connectivity. This is especially important in light of the increasing development in the area, including the erection of fences (Løvschal et al., 2017) and the tarmacking of a main road that passes through this region. It is however important to note that while increasing the amount of land that is protected can benefit wildlife, it can also have a negative conservation outcome if local people become resentful, especially if they are displaced or access to resources are restricted. Land protection schemes should therefore not only take the needs of the wildlife into account, but also those of the people if conservation is to be successful (Roe, 2008).

Acknowledgements

A component of this study was carried out in fulfilment of the Wild Animal Biology M.Sc. degree (EKM) at the Royal Veterinary College and the Zoological Society of London. We thank the National Council for Science and Technology, Narok County Government and the Maasai Mara Wildlife Conservancies Association for permission to carry out this study. We are grateful to Basecamp Foundation Kenya for providing funding to allow us to conduct these interviews. Additional funding was provided through donations given to the Kenya Wildlife Trust. We would like to thank the ten interviewers for conducting the interviews, the respondents for volunteering their time, Fiona Tande for assisting with data entry and Britt Klaassen for mapping the human development. We would also like to thank Sam Turvey for his advice on using interview data and Lianne Petracca for her advice on site-occupancy modelling. Additionally, we thank the reviewers for their useful comments which have greatly improved our manuscript.

Author contributions

Conceived and designed the study: FB. Supervised data collection: FB. Data validation: FB and EKM. Analysis: EKM. Wrote the paper: EKM. Reviewed and edited the paper: FB.

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520

521 **Biographical sketches**

522 **Emily Madsen** undertook this project as part of her MSc degree and it has broadened her interest in
 523 the conservation of carnivore populations, particularly in human dominated landscapes.

524 **Femke Broekhuis** is interested in the ecology and conservation of large carnivores on a landscape
 525 level.

526

527 **Tables**

528 Table 1. Environmental covariates hypothesised to influence the probability of habitat use including
529 the effect for each species.

Category and Prediction	Source
Human presence	
<i>All species will avoid human presence with leopard showing the lowest level of avoidance</i>	1, 2, 3
Proportion of fenced area	
<i>Elephants will avoid area with a high proportion of fenced area</i>	4
Habitat type preference	
<i>Cheetah will select for open habitat but all other species will select for semi-closed</i>	2, 5, 6, 7, 8, 9
Protected Areas	
<i>Cheetah, elephant, lion and wild dog will all have a preference for sites closer to protected areas, the effect will not be as strong for hyaena and leopard</i>	1, 2, 3, 6, 10, 12
Distance to rivers	
<i>Elephant, leopard, lion and wild dog will all select for areas closer to rivers</i>	7, 8, 13, 14

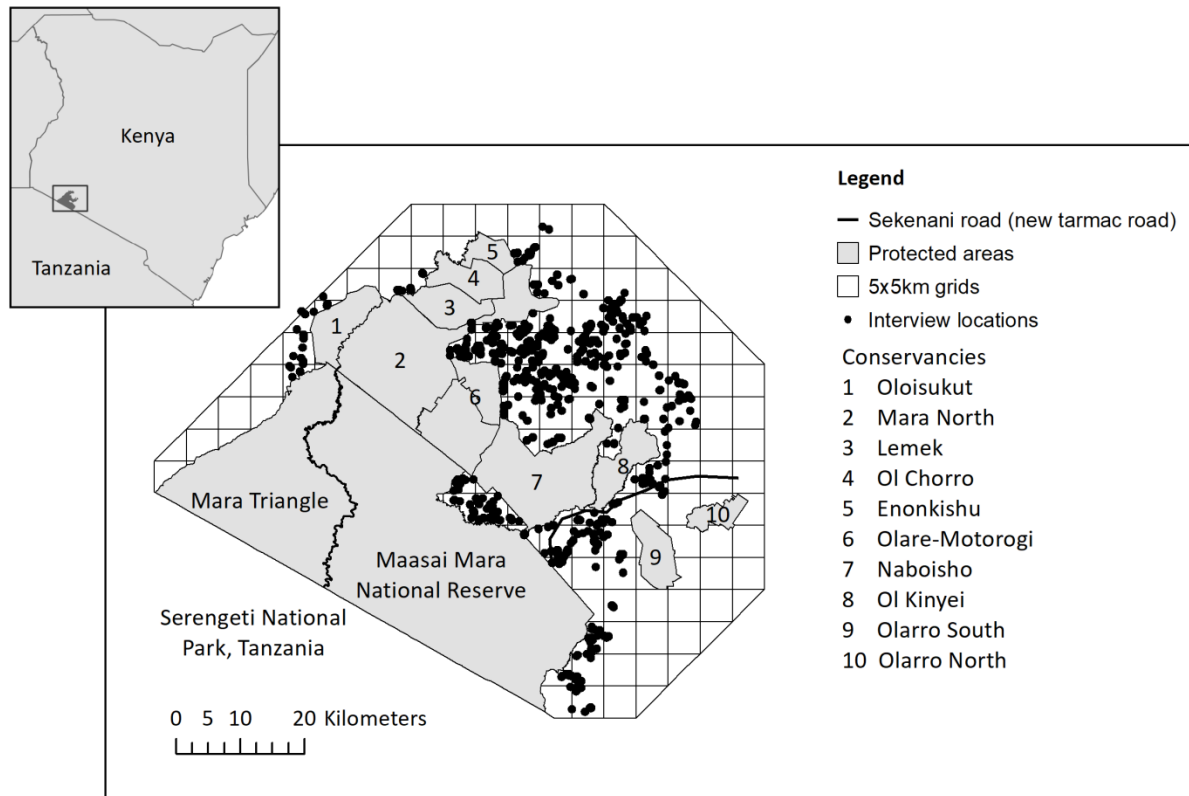
530 Sources: 1 (Schuette et al., 2013; Loveridge et al., 2017), 2 (Galanti et al., 2006), 3 (Athreya et al., 2013), 4 (Loarie et al.,
531 2009; Thouless & Sakwa, 1995), 5 (Bissett & Bernard, 2007; Broekhuis et al., 2013), 6 (Kolowski & Holekamp, 2009), 7
532 (Balme et al., 2007; Balme et al., 2017), 8 (Hopcraft et al., 2005), 9 (Creel & Creel, 1998; Carbone et al., 2005), 10 (Klaassen,
533 2017), 11 (Douglas-Hamilton et al., 2005), 12 (Woodroffe & Ginsberg, 1998), 13 (De Knegt et al., (2011), 14 (Cozzi, 2012)

534 Table 2 The averaged top models for the six species with their AICs and the intercepts and coefficients for site use and detection probability covariates with
535 standard errors. “X” indicates that occupation was one of the detection covariates for that species.

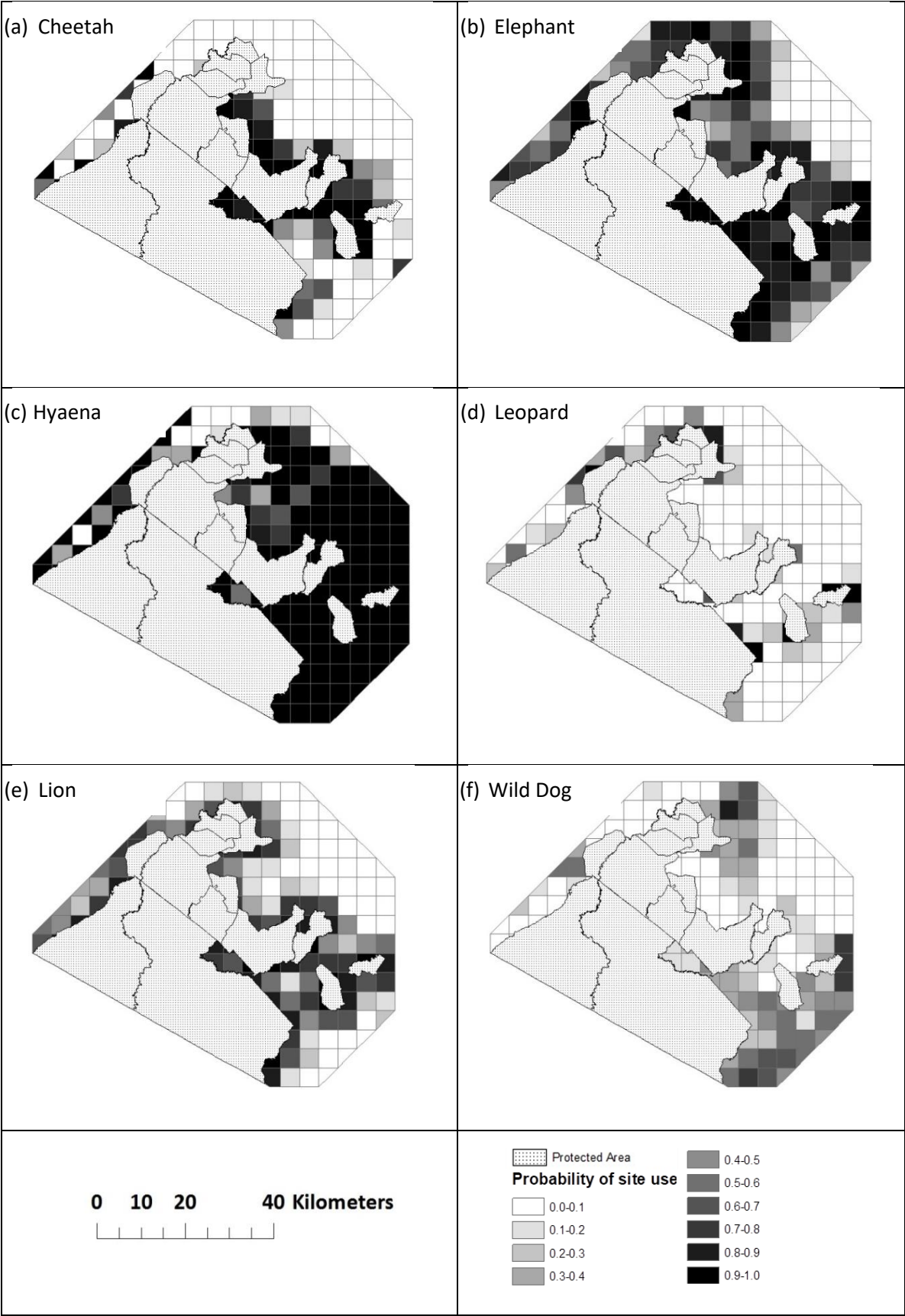
Species	Model	AIC	Δ AIC	Wgt.	Detection Covariates			Occupancy Covariates						
					Intercept	Occupation	Open	Intercept	PA Dist (km)	Human Dist (km)	Fenced Prop	River Dist (km)	Open	Semi-closed
Cheetah	$p(OP). \psi(PA + HumDist + OP)$	305.72	0	0.42	1.94 (1.26)	-	-3.43 (2.08)	8.49 (6.76)	-4.68 (3.84)	31.59 (15.08)	-	-	10.97 (7.15)	-
	$p(OP). \psi(HumDist + OP)$	305.76	0.03	0.41	1.50 (1.10)	-	-2.72 (1.74)	15.60 (7.63)	-	40.00 (17.52)	-	-	11.90 (5.71)	-
	$p(OP). \psi(PA + HumDist)$	307.53	1.81	0.17	-1.16 (0.82)	-	2.07 (1.47)	13.09 (8.84)	-3.46 (2.80)	28.24 (14.54)	-	-	-	-
Elephant	$p(oc + OP). \psi(PA + river + OP)$	420.77	0	0.38	-0.02 (0.54)	X	2.17 (0.96)	-5.85 (2.81)	-3.97 (1.75)	-	-	-25.84 (11.49)	-2.67 (1.87)	-
	$p(oc + OP). \psi(PA.river)$	421.01	0.24	0.33	0.04 (0.57)	X	2.02 (0.92)	-7.06 (2.71)	-3.02 (1.38)	-	-	-27.15 (11.05)	-	-
	$p(oc + OP). \psi(fence.river)$	422.66	1.89	0.15	0.09 (0.55)	X	1.98 (0.86)	-7.82 (5.18)	-	-	-47.39 (29.08)	-39.13 (20.68)	-	-
	$p(oc + OP). \psi(PA + fence + OP + river)$	422.72	1.95	0.14	-0.03 (0.54)	X	2.18 (0.95)	-6.23 (3.26)	-3.90 (1.75)	-	1.78 (8.14)	-27.10 (12.92)	-2.56 (1.93)	-
Hyaena	$p(oc). \psi(PA + river)$	237.95	0	0.56	11.14 (72.3)	X	-	84.75 (40.88)	0.0512 (1.52)	133.93 (65.30)	-	-	-	-
Leopard	$p(oc + OP). \psi(PA + OP)$	355.34	0	0.45	-0.91 (1.35)	X	-0.89 (2.61)	-5.36 (3.13)	-12.67 (5.94)	-	-	-	-13.06 (5.90)	-
	$p(oc + OP). \psi(PA + HumDist + OP)$	355.98	0.64	0.33	-0.70 (1.37)	X	-1.44 (3.00)	-0.44 (4.91)	-13.53 (6.63)	9.50 (8.78)	-	-	-14.01 (7.18)	-
Lion	$p(OP). \psi(PA + SC)$	521.50	0	0.20	-1.05 (0.34)	-	2.88 (0.66)	-5.44 (2.77)	-6.88 (2.88)	-	-	-	-	4.63 (3.64)
	$p(OP). \psi(PA)$	521.77	0.27	0.18	-0.77 (0.40)	-	2.52 (0.77)	-2.71 (1.42)	-4.88 (2.09)	-	-	-	-	-
	$p(OP). \psi(PA + HumDist)$	521.79	0.29	0.18	-0.88 (0.40)	-	2.65 (0.76)	8.60 (9.94)	-3.88 (2.06)	18.12 (15.92)	-	-	-	-
	$p(OP). \psi(PA + HumDist + river)$	521.84	0.33	0.17	-0.92 (0.39)	-	2.70 (0.76)	8.04 (10.84)	-4.02 (2.54)	22.47 (18.51)	-	-12.10 (9.29)	-	-
	$p(OP). \psi(PA + HumDist + SC)$	522.30	0.80	0.14	-1.07 (0.32)	-	2.90 (0.64)	4.72 (10.25)	-5.96 (3.03)	16.03 (15.58)	-	-	-	4.24 (3.69)
	$p(OP). \psi(PA + river)$	522.37	0.87	0.13	-0.78 (0.40)	-	2.54 (0.77)	-4.93 (2.56)	-5.27 (2.37)	-	-	-7.89 (6.70)	-	-
Wild Dog	$p(OP). \psi(SC + river)$	272.83	0	0.46	0.41 (0.67)	-	-0.51 (2.19)	-11.90 (4.40)	-	-	-	-27.18 (12.9)	-	5.17 (2.40)
	$p(OP). \psi(PA + SC + river)$	274.60	1.77	0.19	0.48 (0.75)	-	-0.70 (2.37)	-11.94 (4.45)	-0.58 (1.23)	-	-	-26.12 (13.01)	-	5.24 (2.43)
	$p(OP). \psi(fence + SC + river)$	274.63	1.80	0.19	0.39 (0.64)	-	-0.49 (2.14)	-11.44 (4.59)	-	-	-7.04 (17.18)	-	-	5.10 (2.40)
	$p(OP). \psi(river)$	274.81	1.97	0.17	1.42 (0.51)	-	-4.99 (1.68)	-6.46 (2.95)	-	-	-	-20.94 (10.99)	-	-

Figures

Fig. 1 Study area showing the interview locations outside the protected areas of the Maasai Mara, Kenya, which was divided into the 5x5km sites for the false positive occupancy analysis.

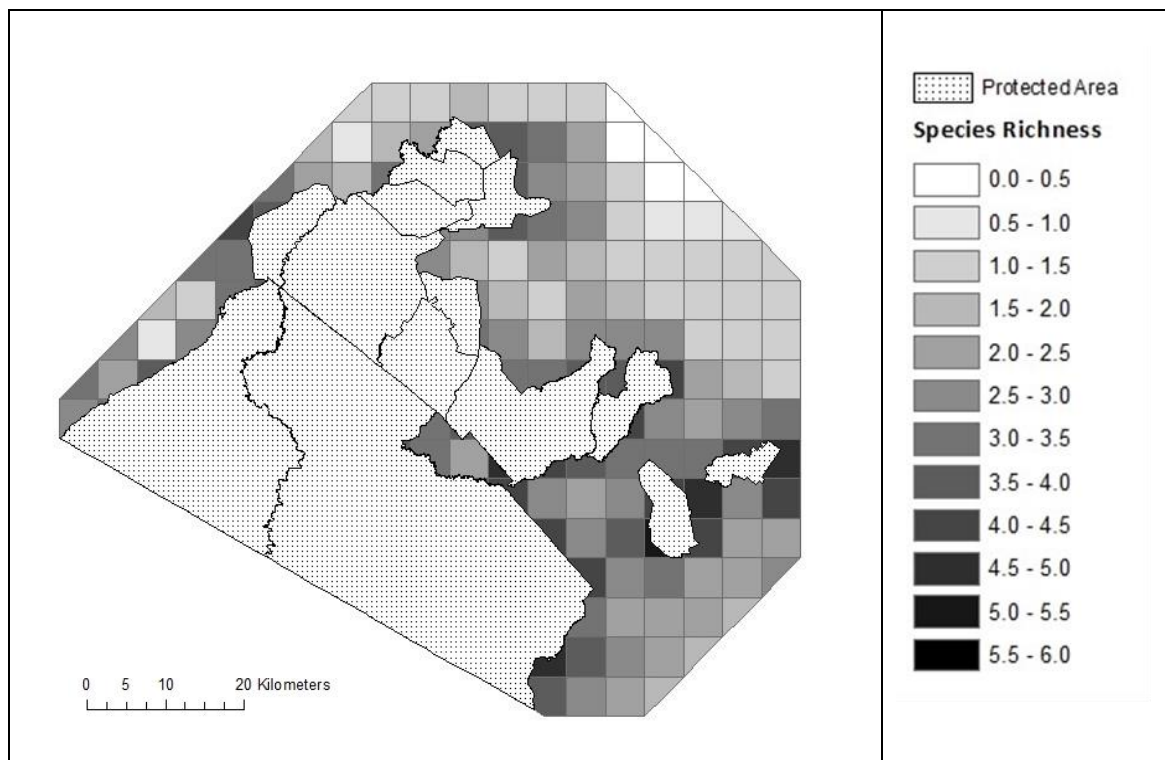


541 Fig. 2 Site use maps for cheetah, elephant, hyaena, leopard, lion and wild dog outside of the protected areas in
 542 the Maasai Mara for sites which are 5x5Km.



543

544 Fig. 3 Species richness map showing the combined probability of site use values for the six species; cheetah,
545 elephant, hyaena, leopard, lion and wild dog, outside the protected areas in the Maasai Mara, Kenya.



546

547 Supplementary Material

548 Appendix A – False positive model selection

549 Table A1. Table of the abbreviations used in the model selection tables.

Abbreviation	Meaning
PA	Mean distance from protected area
SC	Semi-closed and Closed habitat proportion
OP	Open habitat proportion
Fence	Fenced proportion
HumDist	Mean human distance
HumSum	Human density sum
HumMean	Human density mean
River	Mean distance to a river
Oc	Occupation of the interviewee
$p(\dots)$	Detection probability covariates
$\psi(\dots)$	Site use probability covariates

550

551 Cheetah

552 Table A2. Detection probability covariate model selection showing untransformed estimates.

Model	AIC	Δ AIC	AIC weight	Cum. weight	Log-Likelihood
$p(OP).\psi()$	313.00	0.00	0.93	0.93	-151.50
$p(oc).\psi()$	318.33	5.34	0.06	1.00	-153.17
$p(oc + OP).\psi()$	326.85	13.85	0.00	1.00	-156.42
$p().\psi()$	361.72	48.73	0.00	1.00	-177.86

553

554 Table A3. Habitat type covariate model selection showing untransformed estimates.

Model	AIC	Δ AIC	AIC weight	Cum. weight	Log-Likelihood
$p(OP).\psi(OP)$	313.25	0.00	0.55	0.55	-150.63
$p(OP).\psi(SC)$	313.65	0.40	0.45	1.00	-150.83
$p().\psi()$	361.72	48.47	0.00	1.00	-177.86

555

556 Table A4. Human presence covariate model selection showing untransformed estimates.

Model	AIC	Δ AIC	AIC weight	Cum. weight	Log-Likelihood
$p(OP).\psi(HumDist)$	308.26	0.00	0.78	0.78	-148.13
$p(OP).\psi(fence)$	311.55	3.29	0.15	0.93	-149.78
$p(OP).\psi(HumMean)$	314.33	6.07	0.04	0.97	-151.17
$p(OP).\psi(HumSum)$	314.80	6.54	0.03	1.00	-151.40
$p().\psi()$	361.72	53.46	0.00	1.00	-177.86

557

558 Elephant

559 Table A5. Detection probability covariate model selection showing untransformed estimates.

Model	AIC	Δ AIC	AIC weight	Cum. weight	Log-Likelihood
$p(\text{oc} + \text{OP}).\psi()$	439.88	0.00	0.95	0.95	-212.94
$p(\text{oc}).\psi()$	446.67	6.79	0.03	0.98	-217.33
$p(\text{OP}).\psi()$	447.75	7.88	0.02	1.00	-218.88
$p().\psi()$	487.18	47.31	0.00	1.00	-240.59

560

561 Table A6. Habitat type covariate model selection showing untransformed estimates.

Model	AIC	Δ AIC	AIC weight	Cum. weight	Log-Likelihood
$p(\text{oc} + \text{OP}).\psi(\text{OP})$	441.67	0.00	0.52	0.52	-212.83
$p(\text{oc} + \text{OP}).\psi(\text{SC})$	441.79	0.12	0.48	1.00	-212.89
$p().\psi()$	487.18	45.51	0.00	1.00	-240.59

562

563 Table A7. Human presence covariate model selection showing untransformed estimates.

Model	AIC	Δ AIC	AIC weight	Cum. weight	Log-Likelihood
$p(\text{oc} + \text{OP}).\psi(\text{fence})$	431.24	0.00	0.96	0.96	-207.62
$p(\text{oc} + \text{OP}).\psi(\text{HumDist})$	437.87	6.63	0.03	0.99	-210.94
$p(\text{oc} + \text{OP}).\psi(\text{HumMean})$	441.75	10.51	0.00	1.00	-212.87
$p(\text{oc} + \text{OP}).\psi(\text{HumSum})$	441.75	10.51	0.00	1.00	-212.88
$p().\psi()$	487.18	55.94	0.00	1.00	-240.59

564

Hyaena

Table A8. Detection probability covariate model selection showing untransformed estimates.

Model	AIC	Δ AIC	AIC weight	Cum. weight	Log-Likelihood
$p(\text{oc}).\psi()$	245.39	0.00	0.45	0.45	-117.69
$p(\text{OP}).\psi()$	245.78	0.39	0.37	0.82	-118.89
$p(\text{oc} + \text{OP}).\psi()$	247.18	1.79	0.18	1.00	-117.59
$p().\psi()$	261.06	15.67	0.00	1.00	-127.53

Table A9. Habitat type covariate model selection showing untransformed estimates.

Model	AIC	Δ AIC	AIC weight	Cum. weight	Log-Likelihood
$p(\text{oc}).\psi(\text{OP})$	247.07	0.00	0.63	0.63	-117.53
$p(\text{oc}).\psi(\text{SC})$	248.18	1.11	0.36	1.00	-118.09
$p().\psi()$	261.06	13.99	0.00	1.00	-127.53

Table A10. Human presence covariate model selection showing untransformed estimates.

Model	AIC	Δ AIC	AIC weight	Cum. weight	Log-Likelihood
$p(\text{oc}).\psi(\text{HumDist})$	235.95	0.00	0.94	0.94	-111.98
$p(\text{oc}).\psi(\text{HumSum})$	242.03	6.08	0.05	0.99	-115.02
$p(\text{oc}).\psi(\text{HumMean})$	246.04	10.08	0.01	1.00	-117.02
$p(\text{oc}).\psi(\text{fence})$	246.83	10.88	0.00	1.00	-117.42
$p().\psi()$	261.06	25.11	0.00	1.00	-127.53

572 Leopard

573 Table A11. Detection probability covariate model selection showing untransformed estimates.

Model	AIC	Δ AIC	AIC weight	Cum. weight	Log-Likelihood
$p(\text{oc} + \text{OP}).\psi()$	365.55	0.00	0.47	0.47	-175.77
$p(\text{OP}).\psi()$	366.37	0.82	0.31	0.77	-178.19
$p(\text{oc}).\psi()$	367.00	1.45	0.23	1.00	-177.50
$p().\psi()$	392.44	26.89	0.00	1.00	-193.22

574

575 Table A12. Habitat type covariate model selection showing untransformed estimates.

Model	AIC	Δ AIC	AIC weight	Cum. weight	Log-Likelihood
$p(\text{oc} + \text{OP}).\psi(\text{OP})$	365.03	0.00	0.67	0.67	-174.51
$p(\text{oc} + \text{OP}).\psi(\text{SC})$	366.43	1.40	0.33	1.00	-175.21
$p().\psi()$	392.44	27.41	0.00	1.00	-193.22

576

577 Table A13. Human presence covariate model selection showing untransformed estimates.

Model	AIC	Δ AIC	AIC weight	Cum. weight	Log-Likelihood
$p(\text{oc} + \text{OP}).\psi(\text{HumDist})$	363.46	0.00	0.66	0.66	-173.73
$p(\text{oc} + \text{OP}).\psi(\text{fence})$	366.32	2.86	0.16	0.82	-175.16
$p(\text{oc} + \text{OP}).\psi(\text{HumMean})$	367.50	4.04	0.09	0.91	-175.75
$p(\text{oc} + \text{OP}).\psi(\text{HumSum})$	367.51	4.05	0.09	1.00	-175.75
$p().\psi()$	392.44	28.98	0.00	1.00	-193.22

578

579 Lion

580 Table A14. Detection probability covariate model selection showing untransformed estimates.

Model	AIC	Δ AIC	AIC weight	Cum. weight	Log-Likelihood
$p(OP).\psi()$	535.57	0.00	0.47	0.47	-262.78
$p(oc + OP).\psi()$	535.79	0.23	0.42	0.89	-260.90
$p(oc).\psi()$	538.38	2.81	0.11	1.00	-263.19
$p().\psi()$	588.45	52.89	0.00	1.00	-291.23

581

582 Table A15. Habitat type covariate model selection showing untransformed estimates.

Model	AIC	Δ AIC	AIC weight	Cum. weight	Log-Likelihood
$p(OP).\psi(SC)$	536.90	0.00	0.52	0.52	-262.45
$p(OP).\psi(OP)$	537.09	0.19	0.48	1.00	-262.55
$p().\psi()$	588.45	51.55	0.00	1.00	-291.23

583

584 Table A16. Human presence covariate model selection showing untransformed estimates.

Model	AIC	Δ AIC	AIC weight	Cum. weight	Log-Likelihood
$p(OP).\psi(HumDist)$	527.64	0.00	0.97	0.97	-257.82
$p(OP).\psi(fence)$	535.50	7.86	0.02	0.99	-261.75
$p(OP).\psi(HumMean)$	537.56	9.91	0.01	0.99	-262.78
$p(OP).\psi(HumSum)$	537.56	9.91	0.01	1.00	-262.78
$p().\psi()$	588.45	60.81	0.00	1.00	-291.23

585

586 Wild Dog

587 Table A17. Detection probability covariate model selection showing untransformed estimates.

Model	AIC	Δ AIC	AIC weight	Cum. weight	Log-Likelihood
$p(OP).\psi()$	278.39	0.00	0.51	0.51	-134.19
$p(oc + OP).\psi()$	279.11	0.72	0.35	0.86	-132.56
$p(oc).\psi()$	280.92	2.53	0.14	1.00	-134.46
$p().\psi()$	357.47	79.08	0.00	1.00	-175.73

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589 Table A18. Habitat type covariate model selection showing untransformed estimates.

Model	AIC	Δ AIC	AIC weight	Cum. weight	Log-Likelihood
$p(OP).\psi(SC)$	277.83	0.00	0.58	0.58	-132.91
$p(OP).\psi(OP)$	278.43	0.61	0.43	1.00	-133.22
$p().\psi()$	357.47	79.64	0.00	1.00	-175.73

590

591 Table A19. Human presence covariate model selection showing untransformed estimates.

Model	AIC	Δ AIC	AIC weight	Cum. weight	Log-Likelihood
$p(OP).\psi(HumDist)$	277.98	0.00	0.50	0.50	-132.99
$p(OP).\psi(fence)$	280.12	2.14	0.17	0.67	-134.06
$p(OP).\psi(HumMean)$	280.21	2.24	0.16	0.84	-134.11
$p(OP).\psi(HumSum)$	280.22	2.24	0.16	1.00	-134.11
$p().\psi()$	357.47	79.49	0.00	1.00	-175.73

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