Evaluating the use of Local Ecological Knowledge (LEK) in determining habitat use and occurrence of multiple large carnivores

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DOI 10.1016/j.ecolind.2020.106737

Abstract

Understanding habitat use and distribution of threatened species is a cornerstone of conservation, however many of the techniques available can be resource intensive. One cost-effective method is by collecting information on species presence and absence from people who regularly interact with the area of interest, also known as Local Ecological Knowledge (LEK). However, the reliability of this type of data has been questioned, especially when there is a possibility that the focal species is being misidentified or their presence misreported. This can introduce false negatives, when a species is present but has not been reported, and false positives, when the species has been reported but is not present. These biases are not always accounted for which can result in the under- or overestimation of species presence. To better understand the reliability of LEK data, we compared the outputs of five different analytical techniques to that of a more widely accepted approach, resource selection functions, using GPS collar data from three different carnivore species (African lion *Panthera leo*, cheetah *Acinonyx jubatus* and African wild dog *Lycaon pictus*). Hierarchical models which accounted for the possibilities of both false negatives and false positives most closely matched that of the GPS collar data, especially for the two rarer species; African wild dog and cheetah. Our results show that when both false negatives and false positives are accounted for that LEK can be used as a rapid and cost-efficient tool for assessing threatened species which can be adopted into practical conservation projects.

Keywords: carnivores, GPS collar data, interview survey, local ecological knowledge (LEK), species distribution

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Introduction

Wildlife populations are increasingly pressured by human-induced habitat loss and degradation (Ceballos et al. 2017). Accurately determining species occurrence, habitat use and distribution are fundamental for conservation, especially for threatened and rare species (MacKenzie et al. 2003, Gu and Swihart 2004, MacKenzie and Nichols 2004). However, obtaining robust data for cryptic species can be challenging, especially across large spatial extents or in areas where they occur at low densities, such as outside protected areas (Karanth et al. 2011, Andresen et al. 2014). Carnivores in particular exhibit wide-ranging behaviour and much of the available habitat for many species lies outside protected areas, where conflict with humans occurs (Jackson et al. 2012, Ripple et al. 2014). As a result, many carnivore species have experienced rapid declines as human populations, and their subsequent need for more space, increase (Durant et al. 2017, Wolf and Ripple 2017). Being at the top of the food web, carnivores are sensitive to impacts from human activities and therefore function as an indicator for ecosystem health (Dalerum et al. 2008). As such, methods for determining species distribution that are reliable, repeatable, rapid and resource-light are needed to ensure suitable habitat protection and safeguarding of carnivore populations.

Various field methods have been developed to determine habitat use and occurrence of rare species, including camera trapping (Rowcliffe and Carbone 2008), DNA monitoring (López-Bao et al. 2018), and sign surveys (Gopalaswamy et al. 2012). Another commonly used and widely accepted method is the use of GPS collars (Whittington-Jones et al. 2014, Klaassen and Broekhuis 2018). While these methods can provide accurate spatial data, they can be resource intensive. In contrast, harnessing local knowledge, also known as Local Ecological Knowledge (LEK; Zeller et al. 2011, Riggio and Caro 2017, Petracca et al. 2018) represents a relatively quick and cost-efficient method of collecting data on species presence over large areas. A common method of collecting LEK is by interviewing people about a landscape with which they regularly interact, usually through their daily

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activities (Poizat and Baran 1997, Huntington 2000, Turvey et al. 2014). In the last decade, the use of LEK has proliferated and been used to determine species distributions at scales that range from local (Farhadinia et al. 2018, Madsen and Broekhuis 2018) to national (Riggio and Caro 2017) or multi-national (Turvey et al. 2014). Furthermore, LEK has been applied to determine species' occurrence (Kotschwar Logan et al. 2015, Cullen-Unsworth et al. 2017, Ghoshal et al. 2017), corridors (Zeller et al. 2011), changes in distributions (Cano and Tellería 2013), habitat use (Madsen and Broekhuis 2018), abundance (Anadón et al. 2009) and the effects of habitat fragmentation (Anderson et al. 2007, Braulik et al. 2014).

Despite LEK being a well-established data source in fisheries and avian studies (e.g. Gilchrist and Mallory 2007, Eddy et al. 2010, Taylor et al. 2011, Cullen-Unsworth et al. 2017), its reliability has been questioned for studies on terrestrial mammals (Caruso et al. 2017). Among the major criticisms of LEK are that there may be an inherent bias in what is reported (Caruso et al. 2017), the reliability of an individual's memory (Pauly 1995) and heterogeneity in biases for species depending on their ecology and the attitude of the interviewees to focal species (Caruso et al. 2017). Although some of these concerns have been addressed through standardising interview methodologies (Huntington 2000, Gilchrist et al. 2005) the way that interview data are analysed can vary greatly.

To determine species habitat use and occurrence, LEK data can be used such that a reported sighting, or presence, is recorded as a '1' and no sighting, or pseudo-absence, is recorded as a '0'. These data are often analysed using simple linear models, such as binomial logistic regression (Kotschwar Logan et al. 2015, Teixeira et al. 2015). However, simple linear models do not account for detection probability, which is the probability that a species is detected if it is there. This can be influenced by various factors such as time spent in an area (Petracca et al. 2018), habitat type which may affect the surveyor's ability to detect a species when present (Madsen and Broekhuis 2018), socio-cultural factors of the interviewee which may affect the accuracy of their recollection and

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reporting (Turvey et al. 2015), and the behaviour of the species in question (MacKenzie and Royle 2005). By not explicitly accounting for detection probability, false negatives, where an animal is present but not detected, are not accounted for. This can lead to an underestimation of the species' distribution and potentially inaccurate assumptions about habitat preferences (MacKenzie et al. 2002). More complex linear models can, to a certain degree, account for biases associated with the probability of detection by including factors such as observer or habitat as a random effect (e.g. generalised linear mixed models) (Anderson et al. 2007, Nash et al. 2016). A drawback of linear models is that they do not separate the observation process (detection probability) from the state process (e.g. habitat use and occurrence) and therefore may not fully account for the impact of detection probability (MacKenzie et al. 2002). False negatives can be accounted for by using hierarchical models, such as occupancy models, which separate the observation process from the state process (MacKenzie et al. 2002, Royle et al. 2005).

In addition to false negatives, false positives can also occur when a species has been reported but is not present. This is especially the case with interview data as interviewees may misidentify or misremember sightings (Royle and Link 2006). Not accounting for false positives can result in an overestimation of occurrence (Petracca et al. 2018). False positives can be minimised during the data collection stage by, for example, using photo cards to ensure the interviewee can correctly identify focal species (Zeller et al. 2011, Madsen and Broekhuis 2018) and carefully selecting the most experienced interviewees (Davis and Wagner 2003). Additionally, false positives can be accounted for by using appropriate analytical methods, such as false-positive occupancy models (Royle and Link 2006, Miller et al. 2011, Louvrier et al. 2018). However, although several studies have shown that using models which account for false positives can improve predictions (Miller et al. 2011, Petracca et al. 2018), they are rarely used.

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While LEK is potentially useful for predicting species occurrence, the presence of false negatives and false positives can produce misleading results and therefore the reliability of LEK, especially for mammalian species such as carnivores, needs to be evaluated (Gilchrist et al. 2005, Caruso et al. 2017). As such, there have been a few studies that have compared different hierarchical models to each other (e.g. Petracca et al. 2018), qualitatively assessed results from LEK to direct monitoring (e.g. Gilchrist et al. 2005), compared one analytical method to sign surveys (Farhadinia et al. 2018) or collar data (Shumba et al. 2018a), and evaluated models from simulated data with false positives (e.g. Miller et al. 2011). However, to our knowledge no study has quantitatively compared the outputs from multiple different analytical methods for LEK to outputs from more commonly used methods.

Here we test the validity of using LEK to determine species habitat use and occurrence by comparing the outputs to those of resource selection functions (RSF) using data from Global Positioning System (GPS) collars. RSFs use a binary logistic regression design to compare used habitat to available habitat and, whilst they do still have biases (Frair et al. 2010), are a commonly accepted method of assessing the distributions and habitat use of wildlife (Cagnacci et al. 2010). More specifically, we aim to understand the influence of false negatives and false positives on the outputs we analysed LEK data using five different methods (two linear models and three hierarchical models that account for false negatives and false positives). We test this for three African large carnivores (African lion *Panthera leo*, cheetah *Acinonyx jubatus* and African wild dog *Lycaon pictus*) with different life histories, ecological traits and densities that could influence the probability that they are detected and therefore impact the accuracy of the predictions. We hypothesised that the outputs based on LEK data will vary significantly depending on the analytical method used. In general, we predict that the linear models, which do not explicitly account for false negatives and false positives, would lead to inaccurate selection of covariates and therefore poorly predict species

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occurrence. However, we predict that including a measure of observer bias as a random factor would improve the predictions. We also predict that the outputs from the hierarchical models would better resemble the outputs based on collar data, especially the models that accounted for both false positives and false negatives. In addition, we hypothesised that there will be variation in the outputs of the interview data per species. We predict that the social, large bodied lions would have higher detectability, reducing the effect of not accounting for false negatives and positives so the linear models will perform relatively better than the less social cheetah. As wild dogs are very rare in this system we predict that, even though they are social, their detectability will be low so the hierarchical models will significantly outperform the linear models.

Methods

Study area

The study was conducted in the Maasai Mara (centred at 1°S, 35°E; elevation c. 1,700 m) in southwestern Kenya. The Maasai Mara National Reserve (MMNR) borders the Serengeti National Park in Tanzania to the south and wildlife conservancies to the north. The MMNR and the adjacent wildlife conservancies, which will hereafter be referred to as the wildlife areas (WAs; Fig. 1), are bordered by intensive agricultural land to the west and pastoralist settlement to the east. The communities outside the WAs are predominantly Maasai pastoralists who keep a mixture of cattle, sheep and goats. The human population in the areas surrounding the Serengeti-Mara are estimated to have increased 2.4% per year from 1999 to 2012 (Veldhuis et al. 2019). The MMNR, wildlife conservancies and surrounding unprotected areas are not divided by physical barriers thus allowing for free movement of animals. However, land subdivision has resulted in a proliferation of fences being erected outside the WAs to secure grazing for livestock and there are concerns that these fences might impede the movement of wildlife (Løvschal et al. 2017). The north-western border of

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WAs is characterised by an escarpment which rises to roughly 300m above the plains, while to the north-east of the WAs there is a flat region known as the Pardamat Plains which then rises into the Pardamat Hills. The area to the east of the WAs is characterised by dense vegetation eventually rising to the Loita Hills.

Data collection

<u>*Interview survey*</u>

Data on the presence of lion, cheetah and African wild dog outside the wildlife areas were collected through interviews conducted in June and July 2015. For more details on how interviewees were selected see Broekhuis et al. (2017) but briefly, homesteads were selected randomly and at each location the head of the household was interviewed resulting in all interviewees being male. To ensure species were identified correctly, respondents were asked to identify photographs of the focal species (lion, cheetah and African wild dog) along with other predators (leopard *P. pardus*, spotted hyaena *Crocuta crocuta*, striped hyaena *Hyaena hyaena* and tigers *P. tigris*). Only data from respondents who correctly identified the focal species were included in the analyses. The respondents were then asked how frequently they see lion, cheetah or African wild dog in the area around their homestead in the last year: daily, weekly, monthly, yearly, or never. From each interview one data point per species was created and there was no replication of interviewees. This frequency data was turned into presence/absence data by counting daily and weekly sightings as a presence and all other sightings as an absence. Due to African wild dog scarcity in this area we also included monthly sightings to assist model convergence. The study area was then divided into 5 x 5 km sites, and the sighting data were then converted into a series of detections and non-detections for each site. Data were also collected on respondent's occupation, which could impact the amount of time they spent outside and their alertness for wild animals, and used this as a variable to account

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for detection probability (see Data processing and analysis – Hierarchical models). We expected that pastoralists would have better local ecological knowledge than businessmen due to more frequent interactions with their environment which would increase their detection probability. 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 (see Madsen and Broekhuis 2018 for details).

GPS data

Iridium satellite collars (IR-SAT, African Wildlife Tracking (www.awt.co.za/product/)) were fitted to six sub-adult male lions from 2016 to 2018, six cheetahs from 2015 to 2017 and eight African wild dogs from 2013 to 2017. The lions and cheetahs were immobilised in the Maasai Mara (Kenya) by a Kenya Wildlife Service veterinarian and the African wild dogs were immobilised in Loliondo Game Controlled Area (Tanzania) under a permit from the Tanzania Wildlife Research Institute, whose veterinarians immobilised and collared all animals. All individuals were free-darted from a vehicle using a Dan-Inject CO_2 rifle (DanInject, Denmark). Lions were immobilised using ketamine (1.1–1.2 mg/kg) and medetomidine (0.025-0.04 mg/kg) and reversed with atipamezole (0.125 – 0.20 mg/kg; Kock et al. 2006). Cheetahs were immobilised using a combination of ketamine (2–2.5 mg/kg) and medetomidine (0.07 mg/kg) and reversed with atipamezole (0.35 mg/kg; Kock et al. 2006). Wild dogs were immobilised with Zoletil (4 mg/kg; Van Heerden et al. 1991). In all cases, sedation time was kept to a minimum, typically less than 1 hr. After immobilisation, all individuals recovered fully, showing no signs of distress and no apparent side effects were observed on both the short- and long-term. The lion collars, which weighed 1,200 grams, were fitted with a drop-off mechanism and recorded locations every hour. Collars fitted on cheetahs weighed 400 grams (Broekhuis et al. 2018) and recorded locations every 2-3 hours. The wild dog collars weighed <640

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grams, representing ca. 2.6% of collared animal's body weights, and recorded locations every 4-12 hours during peak activity periods.

Environmental variables

For each of the analyses, the following eight environmental variables, grouped into four categories, were used:

Human disturbance – Per site we calculated four proxies for human disturbance: 1) the proportion of each site that was fenced using data from Løvschal et al. (2017); 2) the average distance to the nearest man-made structure; 3) the mean density of man-made structures and 4) the sum of man-made structures. The latter three proxies were calculated using a human footprint layer which included settlements, livestock enclosures, dams, towns and agricultural land (Klaassen and Broekhuis 2018). To calculate the density of man-made structures, polygons were first drawn around each human development to reflect the size of the structure. The polygons were then converted to points and the density was calculated using the point density function in ArcGIS 10.2.2 (Environmental Systems Research Institute Inc., 2014).

Habitat type – The proportions of open and semi-closed/closed habitat for each site were calculated using the habitat layer from Broekhuis et al. (2017). Open habitat was predominantly characterised by grasslands while semi-closed/closed habitat included Croton thickets (*Croton dichogamous*), Vachellia woodlands (*Vachellia drepanolobium* and *V. gerrardii*) and riparian vegetation.

Wildlife areas - The Euclidean distances to the WAs were calculated and averaged per site.

Rivers distance - The Euclidean distances to rivers were calculated and averaged per site.

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Each of the variables were calculated per 5 x 5 km site and standardised using a z-score transformation with a mean of 0 and a standard deviation of 1 unless it was a proportion. In addition, the variables were tested for collinearity with a threshold of $|r|>0.6$ indicating correlation (Dormann et al. 2013), but no correlations were found.

Data processing and analysis

Habitat use and occurrence based on LEK

Linear Models

We used a simple generalised linear model (GLM) with binomial error structure on the presence/absence data generated from the interviews for each of the three species. In addition, to account for potential biases that could be introduced based on a person's occupation, we used a generalised linear mixed model (GLMM) where the interviewee's occupation was added as a random factor. All the analyses using linear models were conducted using the *lme4* package (Bates et al. 2014).

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Hierarchical Models

The presence/absence data that were collected per site were used to create the detection histories. To aid in model convergence, we randomly reduced the number of interviews per site to a maximum of 10 (Petracca et al. 2018). To determine which factors influenced the detection probability we used two covariates, the proportion of open habitat in a site and the occupation of the interviewee or a combination of the two. As the 5 x 5 km sites were smaller than the average home ranges of the species being assessed, which violates the assumption of closure, psi (ψ) was interpreted as the “probability of occurrence” rather than the “probability of occupancy”. We used a basic single-season occupancy model and two different false positive models. The probability of false positives is expected to increase with the number of interviews per site (Royle and Link 2006). This can be accounted for by including a variable in the model associated with the number of interviews that were conducted. We used two different methods to account for these false positives by including 1) a binary variable where “1” was equal to or more than the mean number of surveys (in this case six) and “0” as less than the mean (Royle and Link 2006, Petracca et al. 2018) and 2) a continuous variable for number of interviews per site, hereafter referred to as the false positive binary (FPbinary) and the false positive count (FPcount) models respectively. All occupancy analyses were performed using the *unmarked* package (Fiske and Chandler 2011).

<u>Habitat use and occurrence based on GPS collar data</u>

Data from the GPS collars were used to determine habitat use and occurrence for each species using resource selection functions (RSF; Manly et al. 2002) where the environmental variables at actual locations (used) were compared to an equal number of random data points (available) that were generated within the extent of the study area (Fig. 1). We compared the used data (1) to the available data (0) using generalised linear mixed models with a binomial error

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structure in the package *lme4* (Bates et al. 2014). We used the Moran's Index to test for spatial autocorrelation. To account for individual variation within the data, we added the individual's ID as a random factor (Gillies et al. 2006).

Covariate Selection, Model Building and Selection

For all modelling methods we used a two-stage process to determine the probability of occurrence for lion, cheetah and African wild dog. For each species, we first conducted a univariate analysis within covariate categories to identify the covariate with the lowest Akaike Information Criterion (AIC) (Burnham and Anderson 2002). If there was only one covariate in the category then it was compared to the null model. If no covariates in a group performed better than the null model, then they were not included in the multivariate stage. The second stage was a multivariate analysis where the best performing covariates were used and all model variations were compared using AIC with their relative support assessed using the ΔAIC and AIC weights. If the top model AIC weight was <0.9 then the probability of occurrence was averaged using a weighted method for all the models with ΔAIC <2 (Burnham and Anderson 2002, Arnold 2010). Unless stated otherwise, parameter estimates are presented with standard errors and were considered statistically significant if the 95% confidence intervals do not overlap zero. All statistical analyses were performed in R 3.4.3 (R Development Core Team 2018) and AICs were compared using package *AICmodavg (Mazerolle 2019)*.

Method comparison

Two different metrics were used to assess which LEK-based model output most closely resembled occurrence based on the outputs from the collar data. Firstly, we used a Kendall's tau-b test with 95% confidence to determine the amount of correlation between the LEK-based and collar-based outputs. A positive Tau value would suggest a positive correlation and values closer to 1

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would indicate a greater similarity between the LEK- and collar-based outputs whilst a negative value would indicate a negative correlation. Secondly, we assessed the presence of positive deviations, when the probability of occurrence predicted by the LEK data was high and collar data low ($P_{interview} \geq (P_{collar} + 0.5)$), and negative deviations when the probability of occurrence predicted by the LEK data was low and collar data high ($P_{interview} \leq (P_{collar} --0.5)$).

Results

A total of 630 people were interviewed in the communities surrounding the wildlife areas and 67 of the 139 sites were sampled (Fig. 1). The total number of interviews used per species varied as they were only included if they correctly identified that species. All 630 interviewees correctly identified lion and of these 158 (25.1%) people reported seeing a lion. Cheetah were correctly identified by 584 people (92.7%) of which 63 (10.8%) reported seeing a cheetah. For African wild dog, 598 people (94.9%) correctly identified the species and 61 (10.2%) reported seeing them. From the collars we obtained 16,602 locations for lions, 10,320 for cheetahs and 1,647 for African wild dogs and the Moran I values indicated that there was no spatial autocorrelation present in the residuals.

For lion, the GPS data predicted that they preferred semi-closed habitat, avoided areas with high human disturbance and preferred areas away from rivers but close to the WAs (Table 2). The LEK data predicted similar habitat preferences to the GPS data. In particular, all five models predicted that lion avoided human disturbance, preferring areas further away from man-made structures, and that they were more likely to use areas close to the WAs. In contrast to the collar-based habitat use, the LEK-based outputs predicted that lion preferred areas close to rivers. A difference was also observed amongst the LEK-based outputs with regards to habitat type. Similar to the collar-based outputs, the three hierarchical models predicted that lion preferred semi-closed

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habitat by either selecting for semi-closed habitat or avoiding open habitat. The two linear models on the other hand predicted that lion avoided semi-closed habitat. However, the hierarchical models indicate that the detection probability was significantly influenced by open habitat, in other words, lion were more likely to be detected as the proportion of open habitat in a site increased (Fig. 2). When comparing the probability of occurrence between the collar- and LEK-based outputs, the outputs from the FPbinary model were most similar (Tau = 0.71), closely followed by the FPcount model (Tau = 0.69; Table 3). However, both these models showed negative deviations meaning that when the collar data predicted a high probability of occurrence, these two models predicted a low probability of occurrence resulting in an underestimation in occurrence when mapped compared to the collar data, which was less evident in the two linear models (Fig. 3).

Data from the GPS collars predicted that cheetah preferred open habitat and areas with low human disturbance (Table 2). Cheetah also preferred areas close to the WAs and close to rivers. For the LEK-based models, the FPcount model only contained the habitat variable and, in contrast to the collar-based outputs, it predicted that cheetah would avoid open habitats. For the remaining LEK-based models the predicted habitat use based on human disturbance and the distance to rivers and WAs was similar to the results from the collars. The only exception was that the top FPbinary models did not include the distance to river variable and the top GLMM models did not include the distance to WAs variable. In terms of habitat type, all the models, apart from the FPcount models, predicted that cheetah were more likely to use areas as the proportion of open habitat increased. The FPcount model predicted that cheetah were most likely to be detected in open habitats (Fig. 2) and by pastoralists. Similarly, the simple occupancy models also predicted the cheetah were more likely to be detected in open habitat whereas the FPbinary model predicted that cheetah were less likely to be detected in open habitats, but this was not significant. The probability of occurrence predicted by the FPbinary model was the most similar to the collar-based results (Tau = 0.63, Table 3) with the

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FPcount models being the least similar. Unlike the lion, the occupancy and FPbinary models overpredicted the probability of occurrence, in other words if these models predicted a high probability of occurrence then the collar data predicted a low probability (Fig. 3). When mapped, and this is especially the case for the occupancy models, it looks like cheetah are widespread and that there is a high probability of occurrence outside the WAs.

For African wild dog, the collar data predicted that they selected areas with semi-closed habitat, avoided areas with a high proportion of fencing and preferred areas that were further away from rivers and WAs (Table 2). The LEK-based models all predicted that African wild dog avoid human disturbance but only the FPbinary models included the proportion of the site that was fenced as a variable. All the LEK-based models predicted that African wild dog preferred areas further away from rivers. Neither of the linear models had the distance to WAs in their top models and in contrast to the collar-based predictions the FPbinary model predicted that African wild dog preferred areas close to the WAs. In terms of habitat type, all the models predicted that African wild dog preferred semi-closed habitat by either having a positive coefficient for semi-closed habitat or a negative coefficient for open habitat. Unlike lion and cheetah, all three hierarchical models predicted that the detection probability for African wild dog decreased with increased proportion of open habitat (Fig. 2). When comparing the probability of occurrence, the outputs from the FPbinary model were the most similar to the outputs from the collar data (Tau = 0.73) whereas all the other models showed very few similarities (Table 3 and Fig. 3). As a result, the mapped probability of occurrence for the collar and FPbinary outputs are very similar (Fig. 4).

Discussion

Method comparison

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For all three carnivore species, the LEK-based models that accounted for both false negatives and false positives were most like the predictions based on data from GPS-collars. The importance of including detection probability was particularly evident for lion. For lion the collar data predicted that they preferred semi-closed habitat however, the LEK-based models that did not account for the fact that detection probability was influenced by habitat (GLM and GLMM) predicted that lion were more likely to use open habitat. Therefore, the outputs from the linear models reflected habitats where lion are more visible rather than areas that they use. Surprisingly, and in contrast to the lion and cheetah outputs, the detection probability for African wild dog decreased as the proportion of open habitat within a site increased. This indicates that African wild dog are less likely to be seen in open habitats, which is unlikely especially as they tend to occur in groups (Frame et al. 1979). It is therefore more likely that African wild dogs are present but that they are being misidentified. In open habitats, sightings can occur over longer distances than in closed habitats, and at longer distances it is possible that African wild dog are mistaken for spotted hyaena or domestic dogs *Canis familiaris* which are common in this study site. This could then lead to the introduction of false negatives in open areas decreasing their detection probability. Similar to cheetah and lion, the results for African wild dog show the importance of including the detection probability as the linear models predicted a low probability of occurrence in areas where the collar data predicted a high probability of occurrence and therefore the distribution of African wild dog is likely to be underestimated if detection probability is not accounted for.

The results also highlight the issues that can occur when an animal is reported, but not present (false positives). For example, for African wild dog the collar based output and the FPbinary models indicated that African wild dog avoided areas of human presence, which is corroborated by previous studies (e.g. Woodroffe 2011). However, the models that did not account for false positives (GLM, GLMM and occupancy) predicted that African wild dog selected for human presence. This

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could be because the probability of false positives increases with more interviews per site (Royle and Link 2006). The way this study was designed we inherently had more interviews per site in areas with more people. Therefore, if this increased probability of false positives was not accounted for, the results may reflect a selection for higher human presence. One way of minimising this bias is by conducting the same number of interviews per site. However, this is often not realistic and therefore the use of models that account for false positives are likely to give better results. Additionally, the hierarchical models for cheetah and African wild dog that did not account for false positives showed an overestimation of occurrence. An overestimation of the hierarchical model compared to results from a sign survey was also seen by Farhadinia et al. (2018). This supports other studies which show that not accounting for false positives can lead to overestimation especially where occurrence records are sparse (Petracca et al. 2018) or the species is wide-ranging (Berigan et al. 2019) like these two species which were only seen by ~10% of the people that were interviewed and are both known to be wide-ranging (Masenga et al. 2016, Durant et al. 2017). This overestimation for cheetah specifically could be, in part, related to misidentification. Cheetah have a similar coat pattern to leopard and as a result the two species can be frequently misidentified (Dickman et al. 2014). Whilst we only used data from respondents who correctly identified the focal species, it is still possible that an animal is misidentified, especially if it was seen fleetingly.

These results show that even if photographs are used to try and minimise misidentification, it is still important to account for possible misidentifications in the analysis as they can affect both false negatives and false positives. Interestingly, we found differences in the outputs from the hierarchical models that include false positives, in particular that the FPbinary model outputs are more similar to the collar data compared to FPcount model. It could be that for small samples it is better to collapse the information on the number of interviews into a binary covariate to minimise overparamaterisation. For example, for lion the Kendall tau-b test indicated that outputs from the

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FPbinary and FPcount model were similar whereas for cheetah and African wild dog the FPcount model had a lower value compared to the FPbinary model. This could be because lion were sighted more frequently compared to cheetah and African wild dog. This suggests that for species which are rarely sighted a simple false-positive covariate should be used, but this requires further investigation.

Limitations

Whilst using collar data means it is possible to obtain a precise location of an individual, collars are often only deployed on a few individuals within a population. In this study collars were only deployed on sub-adult male lions which may not be representative of the whole population. However, it is likely that a high proportion of lion seen in the unprotected areas are dispersing males as they are more likely to utilise community land compared to adult males and females (Elliot *et al.* 2014). In addition, data from collars are often used to investigate habitat selection at a fine-scale i.e. at the location of the GPS point. Whilst the majority of our GPS-based results for lion, cheetah and African wild dog are similar to other studies, there are some differences. For example, in this study cheetahs were found to prefer open habitat whereas recent research has shown that this is not necessarily the case (Klaassen and Broekhuis 2018). However, it is likely that cheetah select semi-closed habitat on a fine scale but that they prefer open habitat at a coarser scale (Klaassen and Broekhuis 2018). This illustrates the importance of considering scale when interpreting habitat use results, especially those based on LEK data where a grid design is needed to obtain repeats. While there are inherent biases associated with the use of GPS collars and RSFs such as fix-rates and location imprecision as discussed in Boyce et al. (2002), and Frair et al. (2010), our aim was not to assess the reliability of these approaches but rather to compare LEK-based results to these more commonly used methods. It is also worth noting that in this study we reduced the number of interviews per site to a maximum of ten for the occupancy models to converge, which means that

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the GLMMs and GLMs had more interviews potentially affecting the results. When using a GLM or GLMM more data will increase the accuracy of the results but hierarchical models on the other hand can struggle to converge with high variation in the number per site (Petracca et al. 2018).

Conclusion

In summary, we show that LEK data can be a reliable method to assess species' habitat use and occurrence. These results contradict those by Caruso et al. (2017) who tested the reliability of using interview data by comparing the outputs to those from camera traps. Based on the low congruence between the two methods they suggested that interview data are not a reliable method to determine the presence of elusive species. However, when analysing the interview data they did not account for either detection probability or false positives. Our results however illustrate the importance of accounting for theses biases when using LEK data, especially for species that are rare, wide-ranging and easily misidentified in the field and when data collection has resulted in an unbalanced sample design. We also show that for species that are rarely sighted and sample sizes are small the use of a binary, rather than a count, variable for the number of interviews is likely to give more reliable results. Not accounting for these biases in the appropriate manner could lead to misleading results. This can be particularly harmful to the conservation of rare species because it can lead to incorrect diversion of limited conservation resources (Jetz et al. 2008) which could lead to local extinction.

In this study we used trained enumerators to collect data but this analytical approach could also be used for citizen scientist projects where volunteers collect data for a specific study (Shumba et al. 2018b). The use of citizen scientists could assist in further reducing the required resources and whilst this study was on a local scale, these methods could be used to cover a larger extent which is particularly important when assessing wide-ranging species that require large areas of contiguous habitat for their long-term survival. With ever increasing pressures on wildlife populations around

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the globe the need for data on species status is increasing (Mace et al. 2018), however, resources are stretched (Field et al. 2005), even with increasing public attention. The ability to rapidly, reliably and cost-effectively assess occurrence of elusive and threatened species is essential to inform conservation decisions. Engaging the local community may well provide a promising way to both obtain LEK and help bridge the gap between research and action (Sauer and Knutson 2008, Brooks et al. 2012).

Acknowledgements

Permissions to collar cheetah and lion were granted by the National Commission for Science, Technology and Innovation (Permit No.: NACOSTI/P/16/69633/10821), the Kenya Wildlife Service (Permit No.: KWS/BRM/5001) and the management of the conservancies. Since the Wild Dog Conservation Project is managed by TAWIRI, collaring permission was granted by the Wildlife Division under the Ministry of Natural Resource and Tourism in Tanzania. 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 would like to thank the Banovich Wildscapes Foundation for funding the cheetah collars, WWF-UK and Kenya for funding the lion collars and the European Union's Horizon 2020 research and innovation program (under grant agreement No. 641918 - AfricanBioServices), PTJ Family Foundations, IPBES and BIOTOPE T. LTD for funding African wild dog collars. In addition, we would like to thank the Africa Wildlife Foundation, Vidda Foundation, BAND Foundation and the donations made through the Kenya Wildlife Trust to cover operational costs. We are grateful to Basecamp Foundation Kenya for providing funding for the interview survey and to the ten interviewers for conducting the interviews, the respondents for volunteering their time and Fiona Tande for assisting with data entry.

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Tables

Table 1 A summary of the models that were used to analyse the LEK data to map habitat use and occurrence of lion, cheetah and African wild dog.

Model	Abbreviation	State process	Occupational bias	Detection process/False negatives	False positives
Linear model	GLM	X			
Generalized linear mixed effect model	GLMM	X	X		
Occupancy	Occupancy	X	X	X	
False positive binary	FPbinary	X	X	X	X
False positive count	FPcount	X	X	X	X

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Table 2 The coefficients and standard errors for the covariates in the top models for the LEK and collar based analyses. **Bold** indicates covariates that were significant, X indicates the model included this covariate but did not provide coefficients and – indicates that no covariates from this category were in the top models

Species	Model	Detection probability covariates		Occurrence probability covariates							
		Open habitat	Occupation	Habitat type	Coefficient	Human disturbance	Coefficient	Rivers	Coefficient	Wildlife area	Coefficient
Lion	GLM	-	-	Semi-closed	-0.44 (0.45)	Distance	4.39 (2.33)	**Distance**	**-9.22 (2.25)**	**Distance**	**-1.55 (0.31)**
	GLMM	-	X	Semi-closed	-0.43 (0.46)	**Distance**	**4.61 (2.32)**	**Distance**	**-9.04 (2.28)**	**Distance**	**-1.56 (0.31)**
	Occupancy	**1.46 (0.42)**	-	Open	-0.24 (2.42)	Distance	18.46 (18.40)	Distance	-4.01 (7.74)	Distance	-1.22 (1.05)
	FPbinary	**2.70 (0.74)**	-	Semi-closed	4.48 (3.66)	Distance	19.06 (16.98)	Distance	-10.21 (8.49)	Distance	-5.16 (2.74)
	FPcount	**2.84 (0.67)**	-	Open	-4.61 (3.46)	Distance	20.14 (16.24)	Distance	-5.84 (8.65)	Distance	-6.43 (2.89)
	RSF	-	-	**Semi-closed**	**2.62 (0.06)**	**Sum**	**-0.67 (0.04)**	**Distance**	**0.09 (0.17)**	**Distance**	**-3.59 (0.06)**
Cheetah	GLM	-	-	**Open**	**3.06 (0.68)**	**Distance**	**14.34 (2.85)**	**Distance**	**-10.46 (2.83)**	Distance	-0.61 (0.46)
	GLMM	-	X	**Open**	**3.28 (0.61)**	**Distance**	**15.25 (2.52)**	**Distance**	**-10.89 (2.74)**	-	-
	Occupancy	**1.80 (0.73)**	-	Open	1.89 (1.61)	**Distance**	**39.21 (16.30)**	**Distance**	**-18.82 (8.68)**	Distance	-1.15 (1.31)
	FPbinary	-1.78 (3.17)	-	Open	10.97 (7.15)	**Distance**	**30.59 (15.00)**	-	-	Distance	-4.32 (3.60)
	FPcount	**5.25 (2.03)**	Pastoralists	Open	-4.78 (3.01)	-	-	-	-	-	-
	RSF	-	-	**Open**	**0.65 (0.08)**	**Sum**	**-12.51 (0.76)**	**Distance**	**-3.99 (0.30)**	**Distance**	**-5.44 (0.19)**
African wild dog	GLM	-	-	**Open**	**-4.44 (0.75)**	Sum	0.62 (0.56)	Distance	-7.30 (3.73)	-	-
	GLMM	-	X	**Open**	**-4.44 (0.75)**	Sum	0.62 (0.56)	Distance	-7.30 (3.73)	-	-
	Occupancy	**-3.81 (1.05)**	-	Open	-1.47 (1.75)	Mean	2.82 (4.88)	Distance	-7.62 (6.76)	Distance	0.23 (0.85)
	FPbinary	-1.35 (2.73)	-	**Semi-closed**	**5.17 (2.41)**	Fenced proportion	-7.04 (17.18)	**Distance**	**-25.65 (12.89)**	Distance	-0.58 (1.23)
	FPcount	**-3.93 (1.01)**	Pastoralists	Open	-1.45 (1.80)	Mean	3.12 (4.82)	Distance	-7.98 (6.87)	Distance	0.53 (0.88)
	RSF	-	-	**Semi-closed**	**2.33 (0.20)**	**Fenced proportion**	**-23.89 (3.01)**	**Distance**	**7.74 (0.88)**	**Distance**	**0.80 (0.10)**

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Table 3 Metrics for comparison of the different methods of analysing LEK-based data to the collar-based outputs **Bold** indicates the model which performed best using that metric.

Species	**Model**	**Kendall's tau-b**		**Deviations**	
		P Value	tau	Positive	Negative
Lion	GLM	< 0.001	0.60	0	11
	GLMM	< 0.001	0.61	**0**	**6**
	Occupancy	< 0.001	0.53	3	16
	FPbinary	**< 0.001**	**0.71**	0	19
	FPcount	< 0.001	0.69	0	43
Cheetah	GLM	< 0.001	0.59	**3**	**0**
	GLMM	< 0.001	0.53	4	2
	Occupancy	< 0.001	0.51	66	0
	FPbinary	**< 0.001**	**0.63**	18	0
	FPcount	< 0.001	0.39	4	7
African wild dog	GLM	< 0.001	0.24	11	40
	GLMM	< 0.001	0.24	11	38
	Occupancy	0.01	0.15	28	0
	FPbinary	**< 0.001**	**0.73**	**0**	**3**
	FPcount	0.01	0.14	28	0

Figures

Figure 1 Study site in the Maasai Mara, Kenya, displaying the interview locations and wildlife areas (WAs).

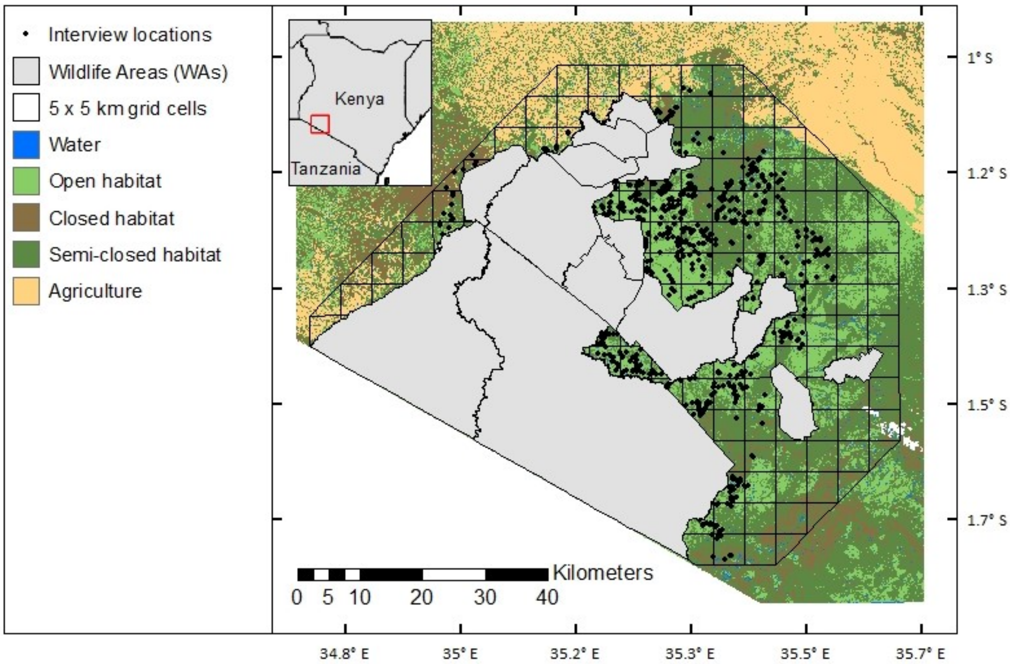

Figure 2 Detection probability and standard errors for the proportion of open habitat for lion, cheetah and African wild dog in the hierarchical models.

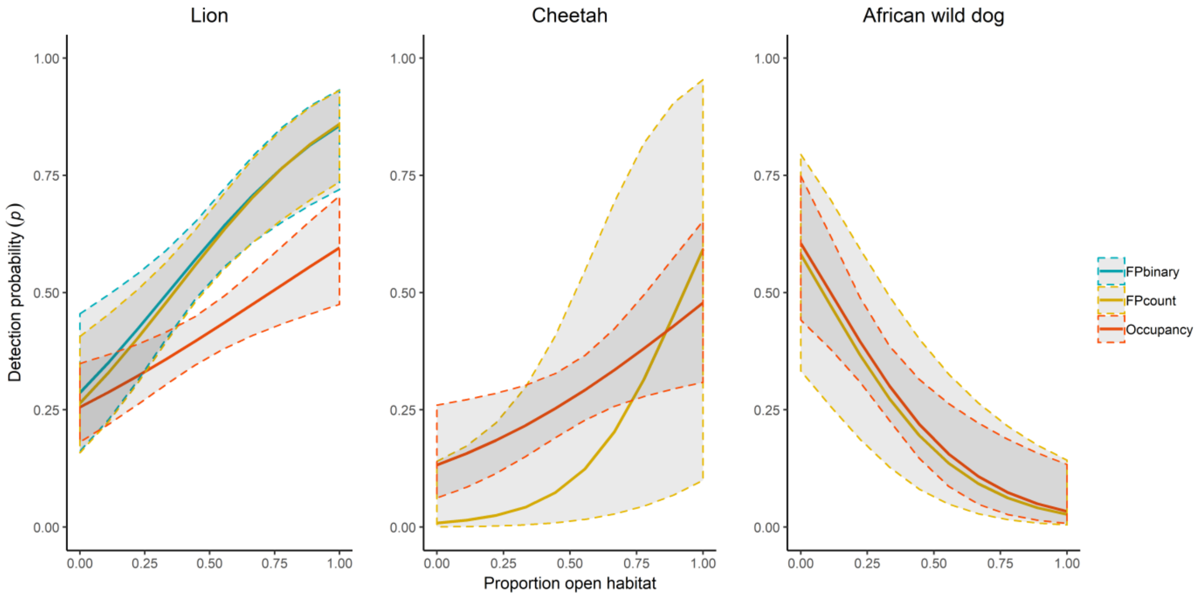

Figure 3 The five different interview analysis method outputs (y-axis) plotted against the collar-based outputs (x-axis) for lion, cheetah and African wild dog for each 5 x 5 km site. The dotted line indicates the LEK-based probability of occurrence predicted is exactly the same as the collar-based probability of occurrence.

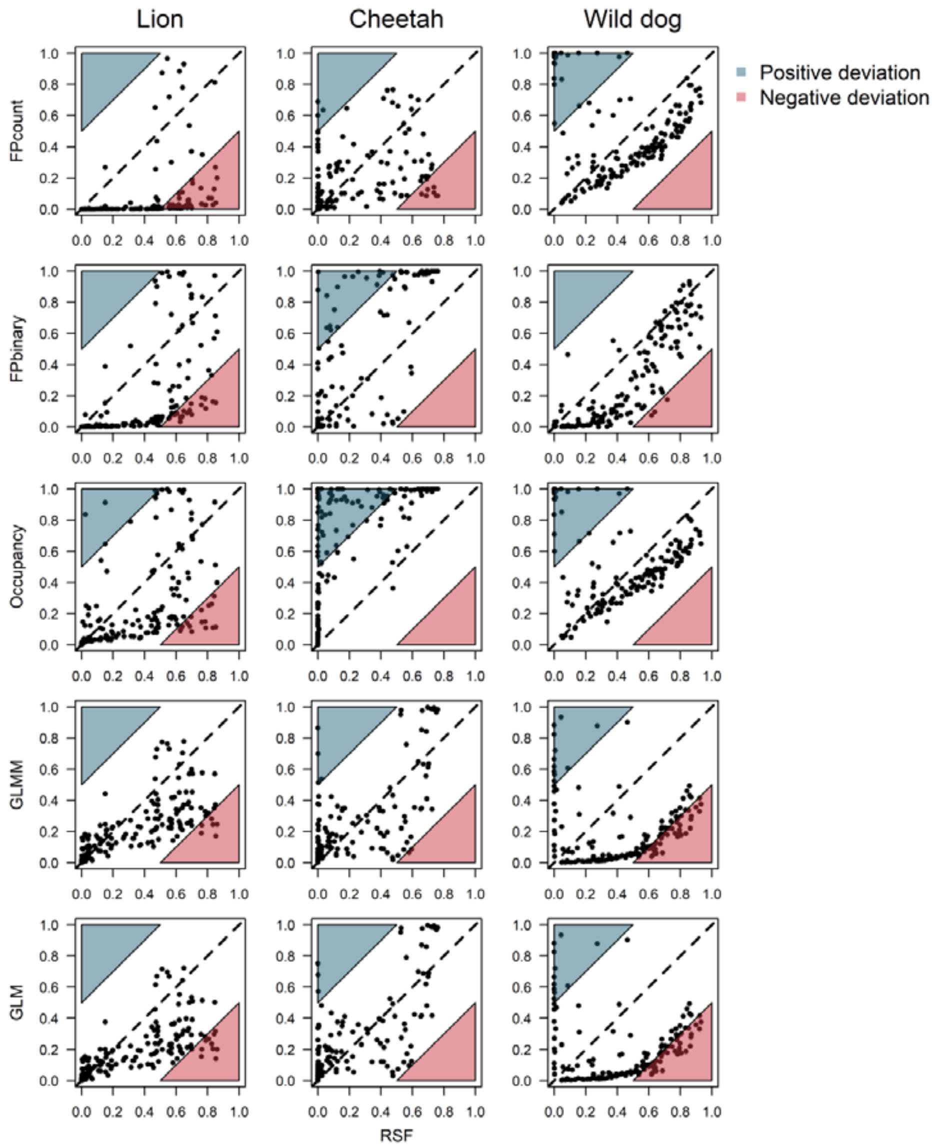

Figure 4 Maps showing the model predictions for occurrence for lion, cheetah and African wild dog for the outputs based on the collar data and LEK data analysed using five different methods; a general linear model (GLM), a generalized linear mixed effect model (GLMM), an occupancy model (occupancy), a false positive binary occupancy model (FPbinary) and a false positive count occupancy model (FPcount).