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RESEARCH ARTICLE

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Combining models for animal tracking: Defining behavioural states to understand space use for conservation

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Abstract

Aim: Rapid advances in technology have created tools able to explore how animals differ in their use of the environment based on behaviour, which can provide insights into the ecology of endangered animals and the threats they face. Though threatened, we know little of vultures' spatial ecology. We examine the external variables that affect vultures' decisions regarding space use, specifically during foraging and feeding when they are at greatest risk for encountering threats, and use this to inform effective conservation interventions.

Location: Tanzania, specifically Southern Tanzanian protected area networks.

Taxon: *Gyps africanus*.

Methods: We tracked 26 African white-backed vultures between 2015 and 2019 in Southern Tanzania. Using hidden Markov models to identify behaviour from raw GPS points and point process models to spatially analyse these behaviours, we tested resource selection decisions in vultures during foraging and feeding, when they are at greatest risk of poisoning.

Results: African white-backed vultures are most likely to forage early in the day outside National Parks, specifically in Game Reserves and Wildlife Management Areas, but avoid areas with high livestock numbers to feed. Eastern and Western populations showed slight differences in preferences, highlighting the need for population level considerations. When not selecting for behaviour, closeness to rivers and habitat openness were more important than protected area status for predicting vulture use.

Main conclusions: Through combining complex analyses, we identified results which simple statistical analyses could not offer. Hidden Markov models and point process models are complementary and can be used to define specific behaviours and associated resource selection. These results provide insight into how animals use their habitat explicitly rather than describing where they spend most of their time. This adds to the growing evidence that although National Parks are important, the management of surrounding areas must be included in conservation efforts.

KEYWORDS
behavioural state, *Gyps africanus*, hidden Markov model, point process model, poisoning, protected area, resource selection, Tanzania, telemetry data, vulture

1 | INTRODUCTION

In our current rapidly changing environment, understanding animal movement and space use can greatly improve conservation efforts and provide insights into threats and species' needs (McKellar et al., 2015). Building on the advancing technology of telemetry that now routinely generates larger, more detailed datasets, new analytical techniques offer unique opportunities to assess questions in spatial ecology. In particular, improved tracking technology (Bridge et al., 2011) and new analytic methods (Patterson et al., 2017) provide novel insights into animal behaviour at unprecedented detail.

For wide-roaming endangered species, tracking data allows us to identify environmental factors that affect dispersal, resource acquisition and ecological threats but to date most analyses focus primarily on describing space use and corridor identification (Bamford et al., 2007; Murn & Anderson, 2008; Phipps et al., 2013). Analyses aimed at more detailed behavioural understanding are so far largely restricted to behavioural science and ecological studies with little direct conservation benefit (Johnson et al., 2013; McKellar et al., 2015; Stein & Georgiadis, 2006; Towner et al., 2016).

Although still relatively new, use of tracking data in conservation studies is rapidly growing (Bridge et al., 2011; Fraser et al., 2018). For example, the identification of previously unknown stop-over sites for long-distance migrants such as the Steppe Whimbrel (*Numenius phaeopus alboaxillaris*) and Sociable Lapwing (*Vanellus gregarious*) are important conservation outcomes (Allport et al., 2018; Donald et al., 2016). Similar collations of tracking data from seabirds have identified areas where foraging overlaps with fishing zones (Bouwhuis, 2018; Carneiro et al., 2020). More detailed behavioural work analysing effects of tour boats on the behavioural state of tagged bottlenose dolphins has helped inform the management of visitors (Lusseau, 2003), and tracking of the Greek tortoise has allowed quantification of the impact of landscape modification on movement and sex-specific behavioural patterns, showing that land use changes have a larger impact on population dynamics than expected because females were much more affected than males (Anadón et al., 2012). Although beneficial, the use of these types of novel analysis techniques to explore tracking data in animal behaviour studies (Patterson et al., 2017) is still not yet well developed in conservation.

While conservation has so far largely concentrated on using movement data for assessment of habitat use, tools are now being developed that allow identification of behaviour classes from GPS data (McKellar et al., 2015). Such analyses enable more nuanced understanding of time budgets and spatial considerations for different types of behaviour, providing deeper insight into animal lives. Two classes of models are gaining particular traction: Hidden Markov models (HMMs: McKellar et al., 2015) and point process models (PPMs: Lindgren & Rue, 2015; Russell et al., 2016). HMMs provide a mechanism for classification of behaviour types and the external factors that influence these (McKellar et al., 2015; Patterson et al., 2017) and have been explored in mammals, insects, fish, and birds (Franke et al., 2004, 2006; Holzmann et al., 2006; McKellar et al., 2015; Towner et al., 2016; van de Kerk et al., 2015). PPMs have recently been used with telemetry data to assess resource selection decisions (Renner et al., 2015) and offer advantages over many presence-only models as they use appropriate spatial resolution and enable assessment of model adequacy (Renner & Warton, 2013), and over traditional regression models as they are spatially explicit and designed for data where locations are known, but absences do not mean inherent unsuitability (Johnson et al., 2013). Together, these methods and the behavioural insights they allow could substantially increase the value of GPS telemetry data within conservation programmes.

Vultures are an ideal candidate for movement studies as they are large, soaring flyers that travel great distances (Alarcón & Lambertucci, 2018; Pennycuick, 1971; Ruxton & Houston, 2004). Because of their considerable size, larger tracking devices can be used on vultures that can last multiple years and provide detailed datasets. Previous work has suggested that several environmental covariates may explain vulture movement patterns (Cone, 1962; Goodwin, 2017). As soaring birds with a high body mass, vultures rely on weather and habitat conditions to keep energy expenditure low while travelling substantial distances, favouring conditions that create thermal air currents and aid in flight (Duriez et al., 2014; Mandel et al., 2008). Previous studies have shown that vultures use substantial areas often incorporating largely unprotected areas (Phipps et al., 2013) and that they do not select for areas with highest food availability or follow large migratory ungulates (Kendall et al., 2014). Partially because of their ability to travel over large areas at low energetic cost, vultures forage with extreme efficiency: in the Serengeti, vultures locate 63% of carcasses compared to 5% for other vertebrates (DeVault et al., 2003; Ruxton & Houston, 2004).

Previous movement studies on vultures have used regression models of gridded occupancy to identify the importance of habitat and legislation on foraging behaviour of the European Cinerous vulture (Arrondo et al., 2018), simulation models to explore population size and density on efficacy of foraging and information transfer in Griffon vultures (Jackson et al., 2008), and minimum convex polygons, fixed kernel density estimations, Brownian bridge methods and grid cell range estimates to determine core foraging ranges and use of protected areas (Kane et al., 2022; Phipps et al., 2013). However, kernel density estimation of distribution models face difficulties such as autocorrelation, irregular time gaps and error in observed locations (Johnson et al., 2011). Movement studies that assume a single behavioural state for animals inhabiting different environmental situations may not give a complete picture, particularly where some behaviours are more relevant to exposure to certain threats (Anadón et al., 2012). Thus, our aim is to build on previous modelling work by combining new analyses methods to incorporate different behavioural states in our consideration of habitat use. A more detailed understanding of vulture movement patterns will have important conservation implications.

Vultures are currently one of the fastest declining bird groups and are of considerable conservation interest (Green et al., 2004; Kruger, 2014; Oaks et al., 2004; Ogada et al., 2016). In the protected areas of southern Tanzania, the critically endangered white-backed vulture is still relatively common, but remains under threat primarily from poisoning (Ogada et al., 2016; Virani et al., 2011). While poisoning occurs for several reasons, in East Africa it is strongly linked to human wildlife conflict, which tends to occur in the boundaries of protected areas, where humans and carnivores overlap (Kolowski & Holekamp, 2006). A study in the Maasai Mara region of Kenya found that human–wildlife conflict was most likely to occur in areas where there was a high proportion of closed habitat and near protected areas (Broekhuis et al., 2017), and another study overlapped distributions of livestock and carnivores to identify potential conflict areas and highlighted protected area border zones as areas of high risk (Santangeli et al., 2019). Vultures, particularly social *Gyps* species, are highly susceptible to poisoning because of their communal feeding, which results in dense aggregations and large-scale mortalities at a single poisoning event (Houston, 2009; Jackson et al., 2008). An important part of enacting protective measures will be to identify foraging and feeding areas to identify key locations where greater conservation action may be warranted and to test whether separate populations show similar behaviours.

Here, we use tracking data from 26 individual vultures captured at five locations across southern Tanzania to identify the behaviour patterns and geography of individual birds that can inform conservation management. We expected to see seasonal and population differences in behaviour (Bosè et al., 2012; Kruger, 2014). We anticipated that flight activities would be concentrated in areas where thermals are common (Duriez et al., 2014; Harel et al., 2016; Pennycuick, 1973) and that foraging would occur in areas with the highest food resource, mainly inside protected areas. We expected the locations of feeding events would be a subset of foraging areas, concentrated in areas with high ungulate densities, and predicted an overall decline in vulture foraging and feeding outside protected areas (Murn & Anderson, 2008; Ogada et al., 2016) to avoid areas with high human habitation and low wildlife density.

2 | MATERIALS AND METHODS

In order to understand vulture foraging decisions, we first collected data on their movements to identify behavioural states using HMMs and then determined the environmental correlates of these specific behaviours using PPMs.

2.1 | Movement data

Between 2015 and 2019, we captured and fitted 26 African white-backed vultures with 70 g microwave telemetry solar-powered ARGOS-GPS units. We trapped and tagged birds in Ruaha and Katavi National Parks and Rukwa and Selous Game Reserves, Tanzania (now partly upgraded to form Nyerere National Park: Tanzania National Parks 2019). Seven birds were tagged in Selous and considered a distinct eastern population, for which the capture location was over 300 km away from the western trap sites in Ruaha and Katavi National Parks. In exploring GPS data, the eastern and western populations showed no interaction or overlap in areas used. Tagging locations for each population are illustrated in Figure 1. GPS units recorded 14 locations at regular hourly intervals during the day from 6:00 AM to 7:00 PM East Africa Time (GMT +3) plus a single overnight point at midnight, with data collection spanning 38–736 days per individual. Since HMM's require regular sampling intervals, we added night-time points as duplicates of the midnight location and assumed this identified the roost site where the bird would stay after sunset until sunrise. The transmitters provide information on velocity, altitude and location. We downloaded movement data from Movebank, and data manipulation, cleaning and analysis were run in R (v 4.0.2, RStudio Team, 2020). We first cleaned movement data to remove erroneous readings from the GPS, which were defined as points with a step length over 106 km per hour (listed as the top speed for this species, Wildlife ACT, 2016). These constituted less than 1% of the data and over 19,000 GPS points were left. We computed height above ground as the difference between GPS height measurements and topographic data and any points with heights estimated below zero were set to NA.

2.2 | Environmental covariates

We collated data on protected area status, livestock density, habitat type, topography, vegetation growth, tree cover and thermal forming potential, all factors previously shown to impact vulture movements (Duriez et al., 2014; Phipps et al., 2013; Santangeli et al., 2019).

For topographic variables, we obtained the digital elevation model (DEM) from the NASA Shuttle Radar Topographic Mission (SRTM) (NASA JPL 2020). We computed slope and aspect (defined as easting, which would obtain the sun/warmth earliest and be best for vultures warming and soaring) from the DEM using the slope and aspect functions in Google Earth Engine (Gorelick et al., 2017). Emissivity and albedo were chosen as factors for thermal forming as land surface emissivity is the efficiency of transmitting thermal energy across the surface into the atmosphere (Agbor & Makinde, 2018) and albedo measures energy that is reflected by a surface, with a low albedo signalling hotter ground temperature and a higher chance of generating thermals (Cone, 1962; Sparrow et al., 1970).

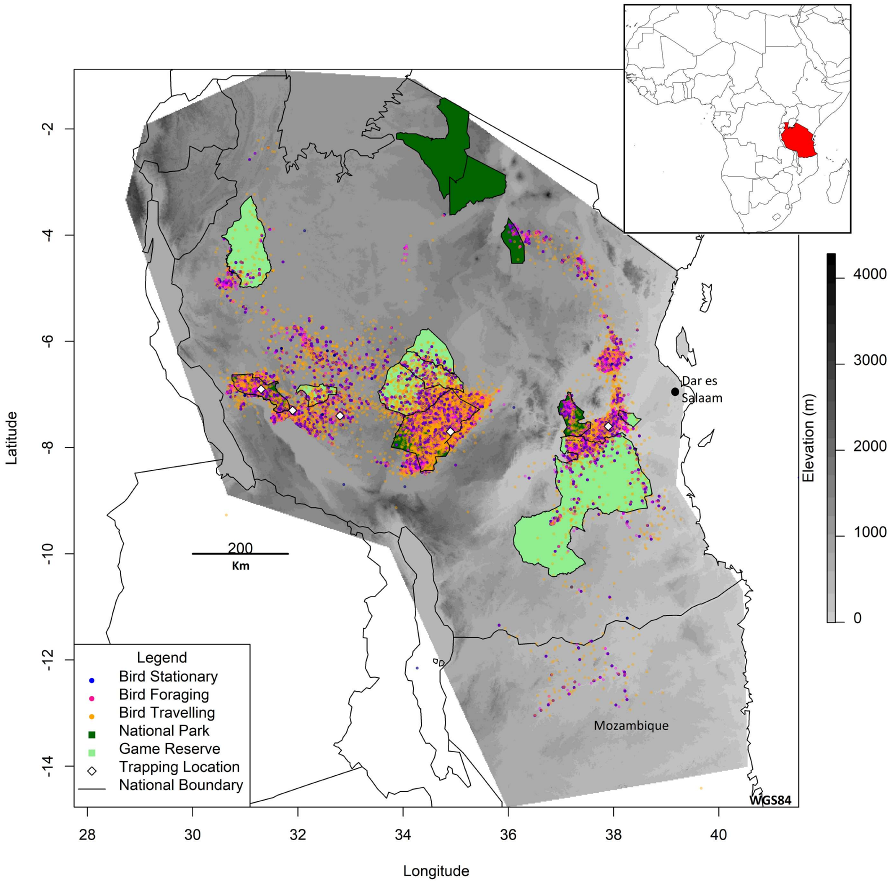

FIGURE 1 Map showing data from all tagged white-backed vultures and major protected areas (green) in Tanzania. GPS points colour coded by behavioural state: Blue is stationary, pink is foraging, orange is travelling. White dots are trapping locations. Eastern and Western populations can be seen to have no overlap in space used.

For habitat, we used the modal value of MODIS habitat data MCD12Q1 v006 from 2015 to 2019 (Friedl & Sulla-Menashe, 2019) and habitat was split into top three land use types: savanna, forest and other. Time was changed to 'time since dawn' starting at 6:00 AM (0) until 5:00 AM the next day (23) and since GPS units only record locations until 7:00 PM and a single point at midnight, we added the missing hours as duplicates of the midnight location. This was done as birds are diurnal and not expected to move overnight. Although it would be possible to model behavioural responses to time of day as a periodic function the use of collars that only transmitted once during the night combined with different expectations of behaviour for morning and evening meant we chose a simpler linear relationship counting time continuously from dawn one day until dawn the next day. Albedo black and white were used to determine areas of high surface reflectance and were retrieved from the mean value of MODIS MCD43A3 v006 for 2015–2019 (Schaaf & Wang, 2015). NDVI were retrieved from the mean of Landsat 8 Collection 1 Tier 1 8-Day NDVI Composite for 2015–2019 (Gorelick et al., 2017) and used to calculate emissivity (a measure of thermal energy transmission) using NDVI following the methods of Agbor and Makinde (2018) and Sobrino et al. (2004).

We used the Hansen UMD global forest change for 2015 (Hansen et al., 2013) to determine percent tree cover. All of the covariates were imported from Google Earth Engine (Gorelick et al., 2017) at a resolution of 100 m and scaled in R for use by subtracting the mean and dividing by the standard deviation. Tropical livestock units were computed from the Food and Agriculture Organization of the United Nations (FAO) ruminant dataset for East Africa 2018 (Robinson et al., 2011). We used a log scale and set values above 100 to NA, as such high values cannot reflect long-term stable densities within the study (around 9.5% of the data exceeded this threshold). Protected area status was created by downloading data from the World Database on Protected Areas (WDPA) (UNEP-WCMC & IUCN, 2019) and ranking protected areas from 1 (most protected) to 4 (no protection status; Table 1).

2.3 | Hidden Markov models

To analyse the data with Hidden Markov models, we computed step lengths and turning angles between known GPS fixes to define behavioural states. Hidden Markov modelling assumes that changes in behaviour, for example from resting to flying, result in consistent changes in step length and turning angle, meaning the combination of these two variables can be used to identify the underlying behavioural state (Patterson et al., 2017). We fitted HMMs using the R package 'moveHMM' (Michelot et al., 2016) first without covariates, assuming between 1 and 6 behavioural states, and compared fit using the Akaike information criterion

TABLE 1 Ranking of protected areas in Tanzania by most (1) to least (4) protected

Protected area status ranking
1. Non-consumptive/non-extractive use only
Tanzania National Parks (TANAPA) National Parks
Ngorongoro Crater Conservation Area
Nature Reserves
2. Consumptive use/extraction permitted
Game Reserves
Wildlife Management Areas
Forest Reserves
National Reserves (Mozambique)
3. Consumptive use/extraction permitted, permanent settlements present
Game controlled areas
Open areas
4.
No protection status

(Table S6). Additional zero-mass parameters were used to address 0 step lengths. Because points overnight were fixed at the roost location, but roosting birds during the day were subject to the usual GPS imprecisions, our model identified these as two statistically separable but ecologically identical states. We therefore consolidated a four-state model with two roosting states to a three-state model with separate behaviours interpreted as sedentary, travelling and foraging, which both fitted the data best and had clearly defined states. Thus the remainder of our analyses were carried out on this three-state model. We then ran the three-state model with added covariates so the state transition probabilities represent functions of the selected covariates. We tried groupings of habitat type, NDVI, tree cover, height above ground, time since dawn, slope, easting (aspect), emissivity and albedo that have previously been shown to affect vulture foraging and flight dynamics though impacts on carcass abundance, carcass visibility and thermal formation, and compared models using Akaike information criterion (Table S1; AIC: McKellar et al., 2015). Finally, we used our fitted model and assigned the most probable behaviour to each fix using the Viterbi algorithm which reconstructs the most probable states sequence (Zucchini et al., 2017).

2.4 | Point process models

Our analysis sought to first identify where birds are found relative to available environment, then identify within this area the covariates associated specifically with foraging, and lastly within foraging areas the factors that were associated with feeding events. Thus, having identified points likely to reflect foraging behaviours in the HMM, we fitted Bayesian Point Process Models (PPMs) using Integrated Nested Laplace Approximation (R package 'INLA': Lindgren & Rue, 2015) to our data. We first modelled the overall pattern of all GPS fixes to identify correlates of bird activity in general, irrespective of behaviour. Then, to determine in detail where foraging behaviour occurs within these broad areas of activity, we modelled the GPS fixes associated with foraging (defined by the HMM) against the background of all non-foraging points to identify where birds spend relatively more time foraging than other activities. Finally, to identify correlates of foraging success where vultures actually feed, we fitted models to the locations where feeding was suspected against a background of all foraging points. We identified likely feeding locations using raw GPS data and a Python tool in ArcGIS, which identifies aggregations by finding all locations where one or more bird was found within a 200-m buffer area between 6:00 and 16:00 hours and without birds moving faster than 1 km per hour.

We defined the spatial extent of the analysis as a non-convex buffer expanded by 100 km around all vulture GPS fixes in Tanzania. Within this, we defined a triangular geographic mesh with nodes separated by 10 km to model spatial dependency (all modelling follows Lindgren & Rue, 2015, with R code supplied). Since we discovered in our exploratory data analysis that birds in the eastern area did not overlap with birds from west of the Great Rift Valley, we tested whether the two populations showed differences in behaviour by including an interaction between the population (based on original capture location east or west of Rift Valley) and each covariate identified by the HMM as likely to influence behaviour (emissivity, albedo and tree cover as a representative vegetation index) as well as with livestock density and protected area status. We incorporated an interaction between season and all covariates to test if behaviour shifts significantly during the wet season (defined as December to May) and dry season (June to December).

3 | RESULTS

3.1 | Behavioural states

The best-fitting HMM included three states: State 1 had a near 0 km per hour step length, which we interpreted as stationary behaviour. State 2 had medium step length (mean of 6.8 km per hour) and no directionality to turning angles, which we described as foraging behaviour. State 3 had a longer step length (mean of 25.2 km per hour) and strongly directional movement indicated by a turning angle distribution with mass centred on zero and so we assigned this as travelling behaviour (Figure 2).

Overall, our HMM indicated that birds spent 75.5% of their time stationary (state 1), 12% foraging (state 2) and 12.5% travelling (state 3). Most transitions from stationary were to foraging and vice versa (Figure 3). Birds shifting from travelling were equally likely to transition to foraging or stationary states (Figure 3). Birds transitioned into and out of a foraging state more than other behavioural states (Figure 3). We found a positive relationship between

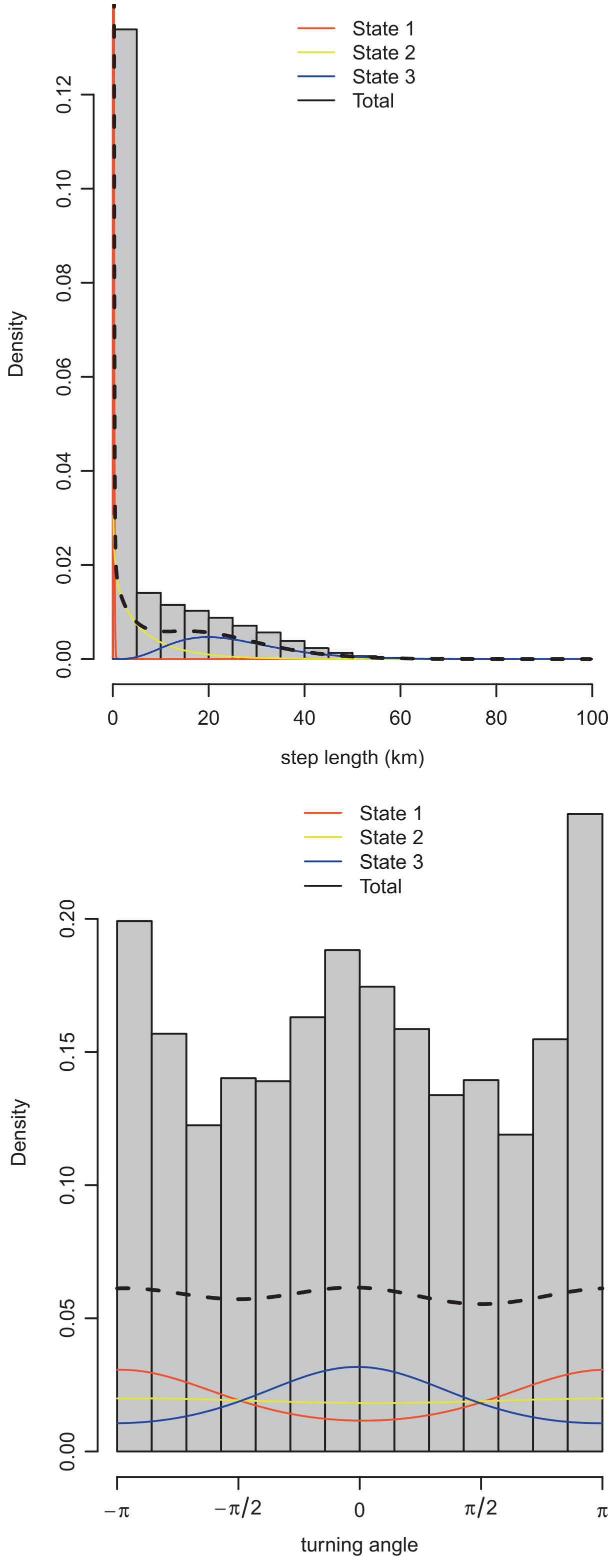

FIGURE 2 Hidden Markov Model step length and turning angle based on behavioural state of white-backed vultures in Tanzania. State 1 (orange) is stationary with a near 0 km per hour step length and high turning angles due to GPS jitter. State 2 (yellow) is foraging with a mean step length of 6.8 km per hour and random turning angle distribution (no directionality). State 3 (blue) is travelling with mean step length of 25.2 km per hour and a turning angle distribution with mass centred on zero indicating relatively high directional movement.

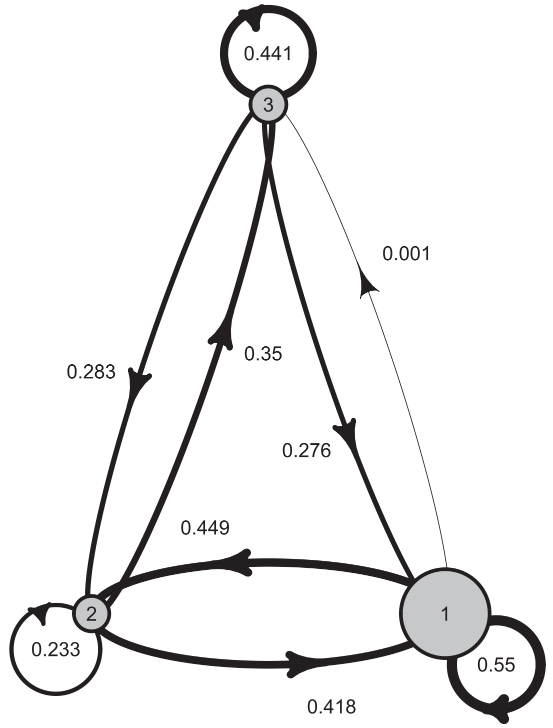

FIGURE 3 Behavioural state transition probabilities as determined by the Hidden Markov Model for white-backed vultures in Tanzania. Filled grey circles are behavioural state (1: Stationary, 2: Foraging, 3: Travelling), and lines depict probability of staying in the same state or moving to another. Same state transitions are low as a consequence of long time intervals between fixes (hourly).

thermal-forming features (emissivity and albedo) and transition to foraging, with an ideal median height above ground and time of day also influencing the probability of foraging (Table S2). We found no evidence that NDVI or habitat was associated with transitions between behavioural states in any model tested (Tables S1 and S2). Mornings (before 12 PM) were most associated with transitions from stationary to foraging and foraging to travelling, while afternoons and evenings showed higher probabilities of transitions of foraging and travelling to stationary. A height of approximately 500–700 m above ground seemed to be ideal for transitions to foraging, but over 1000 m above ground, this drops drastically and travelling becomes more likely (Table S2).

3.2 | Habitat-use analysis

The distribution of raw GPS locations showed that birds from the western population within the Ruaha-Katavi landscape spent 67.9% of their time in National Parks, while birds in the east (from Selous Game Reserve) divided their time between National Parks (43.5%) and Game Reserves (46.9%; Table 2). Geographically, we found very strong matches between the full GPS location data and PPM models of foraging and feeding, suggesting relatively little selection (Figure 4), but the maps show that not all hotspots of vulture activity

TABLE 2 Percentage of GPS points from tagged white-backed vultures in each protected area (PA) rank in Tanzania split by populations (east and west) and behaviour category. Raw number of GPS points in each PA rank were divided by total number of GPS points per population and behaviour for proportion of time spent

	Proportion from total for each population source							
	Western population				Eastern population			
	PA status				PA status			
Source	1	2	3	4	1	2	3	4
Raw GPS	67.9	18.8	5.9	7.4	43.5	46.9	4.6	5.0
Foraging	71.0	17.4	4.6	7.1	40.5	51.2	4.2	4.1
Feeding	63.4	20.3	5.8	10.4	57.6	34.9	4.6	2.9

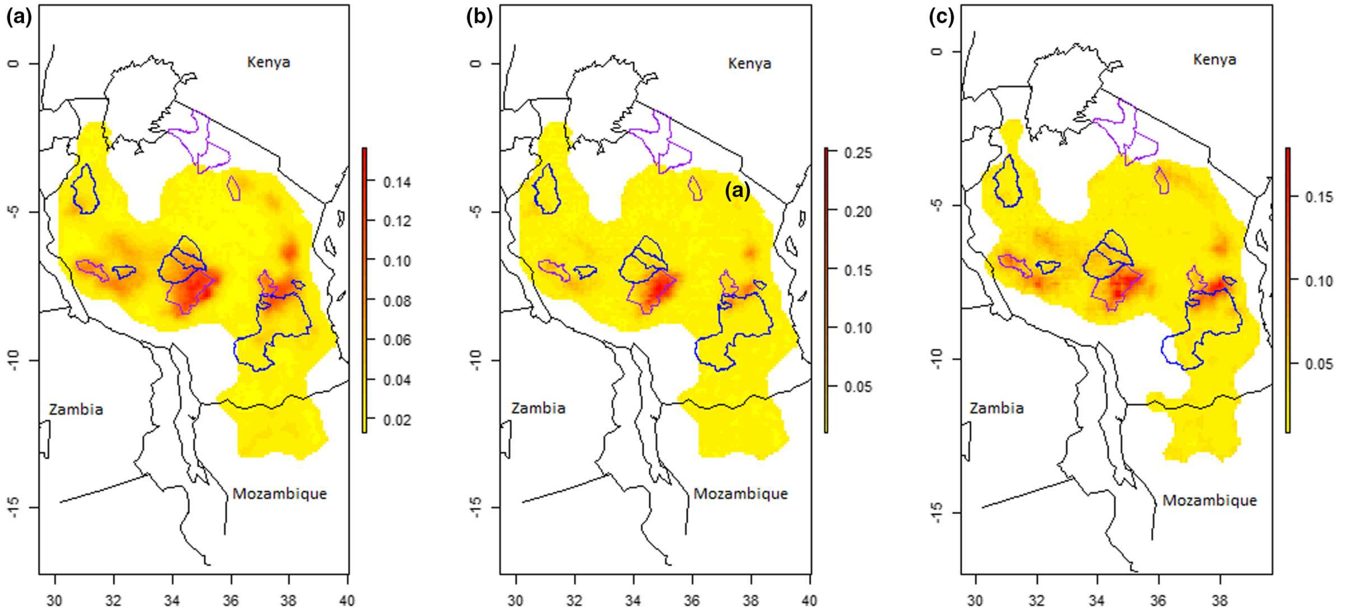

FIGURE 4 Point intensity maps as determined from the Point Process Model for all GPS points (a), foraging (b) and feeding models (c) of white-backed vultures in Tanzania. Red is highest density, which is centred in many protected areas for all models and also covers border zones and corridors between protected areas.

are in protected areas, nor are all parts of protected areas equally used by our vultures. Our first PPM (all GPS points) indicated that vultures in both populations prefer to use areas close to permanent rivers (Ruaha parameter estimate: −0.033 [CI −0.041, −0.024] and Selous estimate not different: −0.009 [CI −0.031, 0.013]) and where livestock density is low (Ruaha estimate: −0.044 [CI −0.07, −0.019], Selous not different: 0.006 [CI −0.057, 0.046]), but this preference decreases during the wet season (Table S3). There was no strong preference for protected area status for either population (Figure 5).

Our second PPM (foraging points using all non-foraging GPS points as background) showed a stronger preference for low tree cover close to rivers when foraging compared to other behaviours, and confirmed the results from our HMM: vultures select for areas with high thermal forming potential for foraging compared to non-foraging behaviours (Table S4). While foraging, vultures showed slightly increased use of Game Reserves and Wildlife Management Areas (WMA) (rank 2) over both National Parks and less protected areas (Figure 5).

Lastly, we ran a PPM with our suspected feeding locations using foraging points as our background. We found that feeding locations were not as correlated with high thermal forming landscapes as foraging locations (Table S5), and that vulture feeding locations were less likely to be associated with game controlled and open areas (rank 3) than expected from foraging locations (Figure 5). Feeding vultures also fed less frequently in areas with high livestock densities than expected from their foraging locations. Interestingly, our PPM results showed that foraging locations were more geographically concentrated than feeding locations, but feeding locations were more likely to occur within National Parks than foraging.

Our PPMs supported an interaction between population and foraging preferences, suggesting differences in foraging behaviour between the two populations (Tables S3–S5). Between the distinct eastern and western populations, the largest differences were in the use of thermal forming areas and livestock abundance. Eastern populations (from Selous Game Reserve) were much more likely to forage in higher thermal-forming areas and forage in areas with higher livestock density compared to the western population (from Ruaha-Katavi landscape). Both populations used Game reserves and WMAs (rank 2) for foraging more often than other behaviours (Figure 5). Feeding locations of the western birds were relatively more frequent

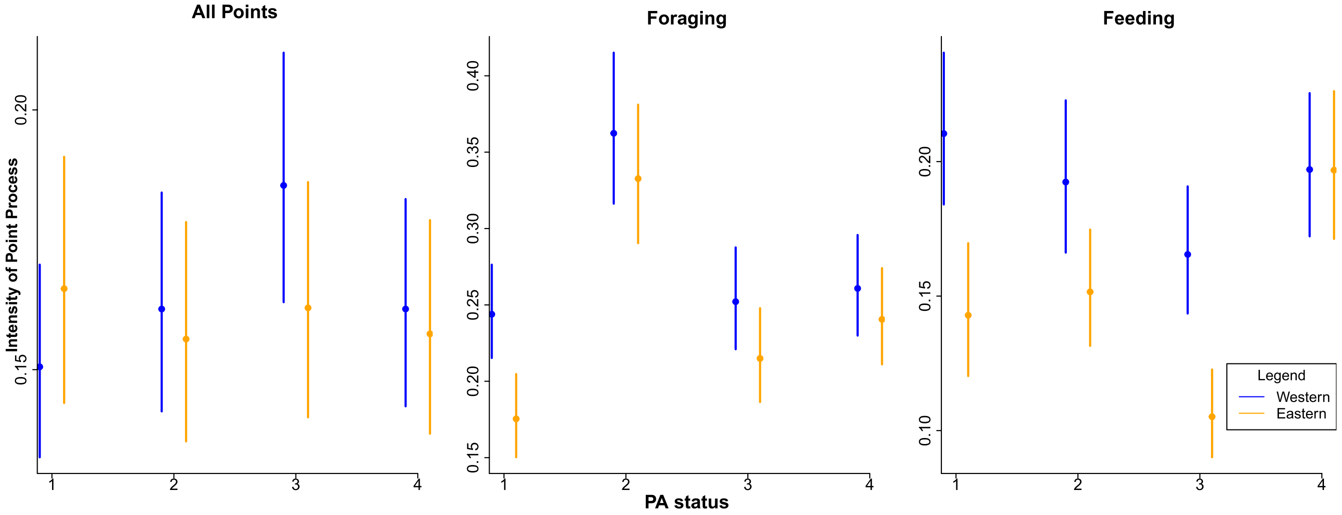

FIGURE 5 Use of protected areas by white-backed vultures in Tanzania based on protected area rank (Table 1: 1 is most protected while 4 is no protection) for different behaviours output by the point process model. Blue is the Western population using Ruaha-Katavi landscape while Orange is the eastern population tagged in Selous Game Reserve.

in National Parks (PA rank 1) than foraging locations indicated, but eastern birds were relatively more likely to feed in unprotected areas (rank 4; Figure 5).

4 | DISCUSSION

Our results highlight the practical insights that can be gained from using new analysis tools with GPS data. For example, the simple distribution of raw data points could give the impression that vultures are largely reliant on National Parks and other strictly protected areas, but our PPM using all points that accounts for spatial autocorrelation indicates that the selection for protected areas is not as strong as the points suggest, with both significant concentrations of activity found outside protected areas and large parts of protected areas rarely visited by vultures. Instead, our overall distribution model indicated closeness to rivers and habitat openness are key features predicting higher occurrence (likely reflecting carcass availability and detection probability), with protected area status of lower relative importance. Similar to other studies, we show that vultures switch to foraging in areas of high thermal availability, within 5 hours of dawn when thermals are more likely, and at a moderate height up to c.1000 m above ground (Duriez et al., 2014; Harel et al., 2016; Pennycuick, 1973). Our feeding analysis highlighted the lack of feeding in areas with high livestock density, suggesting that they avoid cattle as a primary food source and that such areas have low alternative food availability, supporting our initial expectation that vultures avoid dense human habitations. Similar to other studies, we found that overall vulture activity, foraging, or feeding was not restricted to protected areas such as National Parks (Phipps et al., 2013). We found that foraging behaviour was relatively more frequent in Game Reserves and WMAs than expected from overall use, and our feeding models showed that detected carcass locations are more widespread than foraging preferences might have indicated: birds apparently found carcasses in areas where they spent relatively little time foraging, presumably because actual carcass locations are rarely limited to locations ideal for energy-efficient foraging. However, these results did differ slightly between seasons and populations, highlighting the need for detailed understanding of behavioural decision making. Populations showed differences in their foraging and feeding behaviours: the western population from the Ruaha-Katavi landscape strongly avoided livestock areas for foraging and were most successful at feeding in the National Park, while the eastern population's greater use of areas with higher livestock density for foraging and greater use of unprotected areas while feeding may be due to their more substantial movement between protected areas as far apart as Mikumi and Tarangire National Parks. This may lead to greater opportunities to forage in areas of higher livestock density and lower protection status.

Our findings that vultures are most likely to forage in game reserves and WMAs emphasize the importance of these areas for anti-poisoning and conflict management efforts and demonstrate the applications of our analysis results. Because the majority of foraging occurs in the early morning, our results emphasize that patrols aimed at finding poisoned carcasses are unlikely to effectively reduce poisoning risk and instead interventions should be targeted at preventative work: encouraging systemic change in community–wildlife interactions. Through identifying behaviour from raw GPS points and subsequent spatial analyses of these behaviours, we have identified the subtler risk factors of poisoning to vultures as well as their greater reliance on areas outside National Parks for foraging and feeding than a simple use statistics analysis alone would suggest.

Although we were able to obtain important results from these models, we were greatly restricted on GPS sampling frequency and had relatively coarse temporal resolution which might limit our findings. Although hourly fixes are sufficient for studying large scale movement, tracking discrete behaviour changes becomes more difficult. Many behaviours may occur in short time periods; a vulture feeding event can last less than 30 min and thermal soaring can occur in seconds which hourly datasets might miss (Murgatroyd et al., 2018). This highlights the need for consideration of the study organism and sampling at frequencies appropriate to the specific species. For example, while we believe that hourly fixes would capture most vulture behaviour due to their tendency to forage for long periods over large areas, this would not be appropriate for a species with sit-and-wait or stalk-and-ambush movements such as felids or accipiters where behaviours of interest typically last seconds (Cresswell, 1996; Williams et al., 2014). Advanced tracking devices that provide fixes every minute or more and include other features such as accelerometers, can provide incredibly in-depth information into behaviour (Harel et al., 2017; Nathan et al., 2012; Spiegel et al., 2013) and could expand future analyses to include more discrete behaviours like incubation. High-resolution data also allows for more complex statistical models to be applied, which can help to draw a more comprehensive picture of an animal's behaviour. In particular, hierarchical HMMs (Adam et al., 2019; Leos-Barajas et al., 2017) can be used to model multi-scale data in a joint HMM-type model, which allows to infer behavioural modes that manifest themselves at different time scales.

New analytical tools such as HMMs and PPMs can offer great insight into not just habitat use, but how animals differentiate their use of the environment based on behavioural states (Franke et al., 2006; Holzmann et al., 2006; McKellar et al., 2015; Renner et al., 2015; Towner et al., 2016; van de Kerk et al., 2015). In terms of conservation, what animals are doing can be just as significant as habitat use alone, particularly where behaviour will dictate the susceptibility to threats. For vultures, time spent in areas of high poisoning risk is only a threat if vultures are foraging or feeding (Ogada et al., 2016; Santangeli et al., 2017; Virani et al., 2011). Studies that provide insight on how animals use habitat thus have greater value than those only showing where they spend their time.

Until now, conservation studies have largely focused on habitat use of vultures based on analysis of home range or analysing GPS data without distinguishing between behaviours (Bamford et al., 2007; Fischer et al., 2013; Kane et al., 2022; Phipps et al., 2013). We illustrate the value and benefits from using more complex models that allow us to interpret how habitat use changes with behavioural state, thus making findings more relevant to management goals. Without the behavioural distinctions included in our analysis, we would not be able to distinguish that birds forage and feed outside national parks more often than expected from their general movement patterns: an observation that has direct conservation implications. We have shown that HMMs and PPMs are complementary and can be used in this way to define specific behaviours of interest and spatial factors associated with these, which has proven successful for our two distinct populations of vultures in Tanzania.

This study helps to broaden the applications of statistical modelling in the field of movement ecology and how animal tracking data can be used to inform conservation actions. We have shown that vultures provide good example species for spatial resource analysis and the practical applications these results can yield. Our results add to the growing evidence that although protected areas are important, the management of unprotected areas and human settlements must be included in conservation efforts for wide-ranging species such as vultures (Bamford et al., 2009; Broekhuis et al., 2017; Carneiro et al., 2020; Henriques et al., 2018; Monadjem & Garcelon, 2005; Phipps et al., 2013; Pomeroy et al., 2015; Santangeli et al., 2017; Virani et al., 2011).

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CONFLICT OF INTEREST

The authors have no conflict of interest to declare.

DATA AVAILABILITY STATEMENT

The data that support the findings of this study are openly available in Movebank Data Repository at https://www.datarepository.movebank.org/, reference number Study ID 10339440.

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BIOSKETCH

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Author Contributions: CB, MM, CK and NP collected data; NP, CMB and CK conceived the ideas and designed methodology; NP and CMB analysed the data; NP, CK and CMB led the writing of the manuscript. Authors CMB and CK contributed equally to this work and all authors contributed to the drafts and gave final approval for publication.

SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.

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