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# Spatial analysis of aerial survey data reveals correlates of elephant carcasses within a heavily poached ecosystem

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## ARTICLE INFO

## ABSTRACT

Growth of the illegal wildlife trade is a key driver of biodiversity loss, with considerable research focussing on trafficking and trade, but rather less focussed on supply. Elephant poaching for ivory has driven a recent population decline in African elephants and is a typical example of illegal wildlife trade. Some of the heaviest poaching has been in Southern Tanzania's Ruaha-Rungwa ecosystem. Using data from three successive aerial surveys and modern spatial analysis techniques we identify the correlates of elephant carcasses within the ecosystem, from which important information about how poachers operate can be gleaned. Carcass density was highest close to wet-season (but not dry season) waterholes, at higher altitudes and at intermediate travel cost from villages. We found no evidence for an ecosystem-wide impact of ranger patrol locations on carcass abundance, but found strong evidence that different ranger posts showed contrasting patterns in relation to carcasses, some being significantly associated with clusters of carcasses, others showing the expected negative correlation and most showing no pattern at all. Despite a spatial change in elephant carcass locations between years, we find little evidence to suggest poachers have changed their behaviour in relation to key modelled covariates. Our maps of poaching activity can feed directly into anti-poaching control measures, but also provide general insights into how illegal harvest of high value wildlife products occurs in the field, and our spatio-temporal analysis provides a valuable analysis framework for aerial survey data from protected areas globally.

## 1. Introduction

Despite global commitments to halt biodiversity loss, the populations of many species continue to decline (Pimm et al., 2014). Although protecting land in national parks and nature reserves remains a cornerstone of conservation practice, for many species and in many areas, wildlife populations within protected areas are also dwindling (Laurance et al., 2012). A primary cause of ongoing wildlife decline in protected areas is illegal harvesting, with inadequate law enforcement driven by insufficient resourcing and under-motivated staff, exacerbated by corruption of those charged with enforcing laws (Moreto et al., 2015). For some high-value wildlife products such as pangolin scales, rosewood, rhinoceros horn or elephant ivory a thriving international trade has developed that simultaneously endangers the

harvested animal and plant populations (Challender et al., 2015–2017) and provides financial support to criminal gangs that can destabilise local institutions (Bennett, 2015). An apparent increase in elephant poaching over recent years has received significant publicity, with evidence that poaching rates of African elephant *Loxodonta africana* are again driving continental scale population declines (Chase et al., 2016; Wittemyer et al., 2014). This is a particular concern because elephants are ecosystem engineers, facilitating numerous other species in the savannah (Kohi et al., 2011), but their large size and the consequent ease of finding evidence of illegal activity in the form of carcasses also offers opportunities to study usually cryptic patterns of illegal harvest of high-value wildlife commodities.

East Africa is home to several of the largest populations of African elephant: in 2013 the IUCN African elephant specialist group estimated
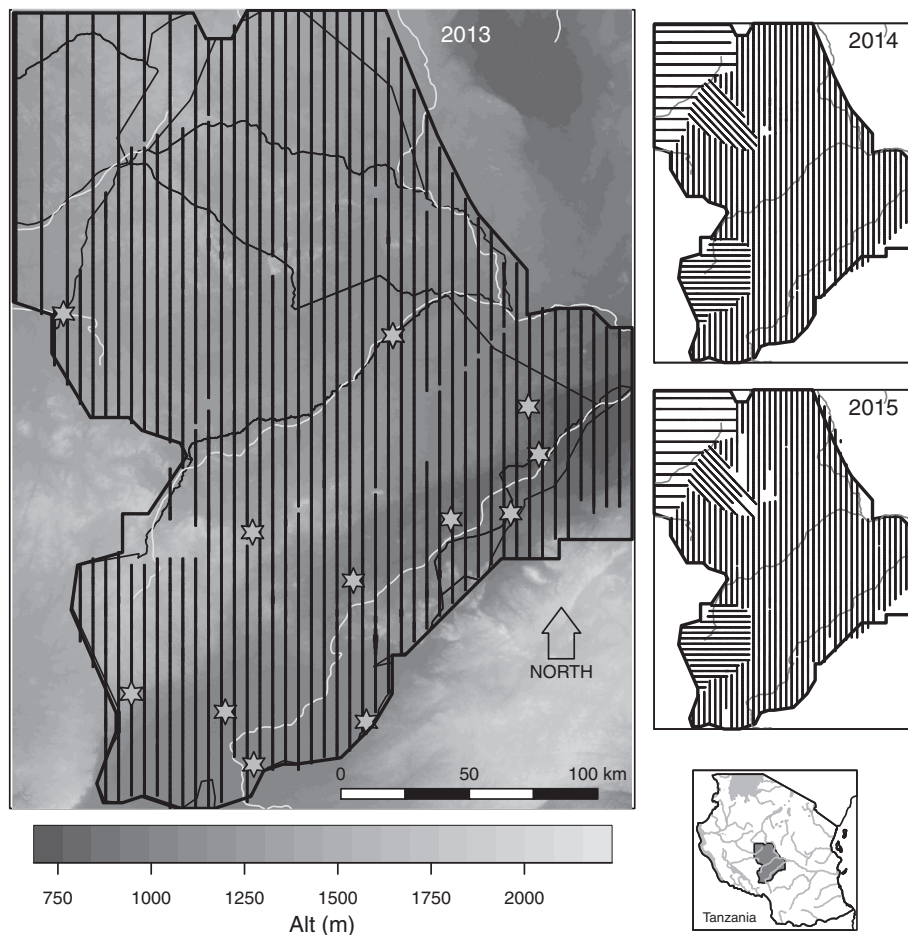
**Fig. 1.** Flightlines for the Ruaha/Rungwa surveys 2013–2015, with map of Tanzania showing detailed region. Background shows altitude. Note changes in alignment in 2014 and minor differences in 2015, main protected areas and rivers and presented with the positions of permanent ranger posts indicated by pale stars in the main panel.

that there were around 400,000 elephants in Africa (IUCN, 2013). In 2009 Tanzania's elephant population within the Ruaha-Rungwa ecosystem was the third largest in Africa, holding nearly 10% of the global population, ranging over 40,000 km² of strictly protected National Park, Game Reserve and Wildlife Management Areas. Recently, however, several lines of evidence suggest this population is in rapid decline due to poaching,with a large majority of elephant carcasses encountered by monitoring teams between 2013 and 2015 resulting from illegal killings (CITES, 2016). Genetic identification of source populations for ivory seized from international smugglers has identified an increase in the harvest coming from southern, then south-western Tanzania (Wasser et al., 2015). Since the largest population of elephants (estimated at 30,500–38,800 individuals in 2006) in southwestern Tanzania is found in the Ruaha-Rungwa ecosystem, it is logical to conclude many are from this population. Simultaneously, aerial surveys tell a story of rapid decline (TAWIRI, 2013, 2014, 2015): a 56% decline between 2009 and 2013, with a further decline of 22–59% to 11,100–20,600 individuals in 2015. (A 2014 survey estimated only 6600–9900 individuals, with at least some of the low numbers in 2014 likely due to the lack of large herds inflating both estimate and confidence intervals: TAWIRI, 2015). These data are strongly suggestive that poaching is having a dramatic effect on the elephant population in the ecosystem, an inference further supported by demographic change in the Ruaha elephant population over the same period (Jones et al., in press). In addition to counting live elephants, the aerial surveys also count carcasses. Carcass counts can be corrected by a standard decay rate to generate a plausibility check of observed declines (Chase et al., 2016; Wells, 1989). These data indicate that the declines between 2009 and 2013 were in agreement with the estimated number of carcasses, whilst the continued decline between 2013 and 2014 was not matched

by the estimated carcass ratio and the apparent population increase to 2015 was accompanied by a further increase in carcasses (TAWIRI, 2013, 2014, 2015). Moreover, at several thousand elephants per year, the implied poaching rate suggests elephant poaching on a near industrial scale, despite active ranger units throughout the ecosystem. The size of this decline and the poaching pressure exerted across Africa suggests that review and redirection of protection effort would be timely.

Aerial surveys are commonly used to survey both terrestrial (e.g. Ogutu et al., 2016) and marine species (Andriolo et al., 2006). Analysis of aerial survey of elephants typically focuses on estimating the number of animals (and carcasses) that are seen across the ecosystem as a whole, and the richness of information contained within the spatial pattern of observed live and dead animals is usually ignored (Booth and Dunham, 2016; e.g. Chase et al., 2016). Since Geographical Positioning System (GPS) technology has become widely available, aerial surveys usually record the location of every animal seen within known observation windows in order to present spatial distribution maps of observation as well as density estimates (e.g. Chase et al., 2016). The presence of spatial information on live and dead elephants in combination with widely available spatial datasets including important covariates makes it possible to use spatial analysis to identify both the correlates of animal and carcass distribution at fine scales (Ndaimani et al., 2016) and to assess how these correlates may change over time. Such spatial analyses can provide insight into the ways poachers are operating within a landscape and have recently been used to identify priority areas for ranger patrols, with potential for dramatic improvement with relatively little investment (Critchlow et al., 2016).

Here, we use Bayesian spatially explicit generalised additive models fitted by integrated nested Laplace approximation (INLA: (Rue et al.,

2009) to analyse the 2013, 2014 and 2015 repeat aerial survey data of elephants in the Ruaha-Rungwa ecosystem. We set out to test the evidence (a) that live elephants have changed their habitat associations between years; (b) that spatial patterns in carcass locations identify changes in poacher activity; and (c) that ranger posts and associated activities are effective deterrents for elephant poachers. In addition, we aimed to identify priority areas for increased law enforcement to minimize future poaching.

## 2. Methods

### 2.1. Study area

The Ruaha-Rungwa ecosystem covers 40,000 km$^2$ of savannah habitats in south west Tanzania (Fig. 1). Habitats consist of extensive flood plains and swamps, with open acacia savannah in lower areas and nutrient poor *Brachystegia* dominated woodlands (Miombo) at higher altitudes. Permanent water is found in the Ruaha river in the south, and in small pools along the Rungwa river in the centre. Rainfall is highly seasonal, concentrated in a single rainy season from December to April, with an average of 580 mm per year at Msembe and slightly increasing rainfall east to west across the ecosystem (Barnes, 1983). During the dry season wildlife congregates near permanent water (in the acacia woodlands at lower altitudes) from where many animals disperse into higher altitude woodlands during the wet season. The ecosystem includes the largest national park in Africa (Ruaha National Park), several contiguous and strictly protected game reserves (Rungwa, Kizigo and Muhesi being the largest) where regulated tourist hunting is the only permitted activity and several smaller wildlife management areas and game controlled areas where restrictions on activities prioritise wildlife conservation within a sustainable use framework (MNRT, 2007). Just 5% of the survey area is unprotected, and although a fast increasing human population surrounds the ecosystem, density is relatively low (NBS, 2012).

### 2.2. Elephant data

Aerial surveys were conducted by a team of professional surveyors in 2013, 2014 and 2015. All surveyors undertook an intensive training session before the survey start in 2013 and the same team undertook the 2014 and 2015 surveys following shorter refresher courses. Each survey followed standard aerial survey methods recommended by Norton-Griffiths (1978) and full details of the implementation within the Ruaha-Rungwa ecosystem are provided in three TAWIRI reports (TAWIRI, 2013, 2014, 2015). In brief, surveys were conducted from three high-wing Cessna single-engine aircraft, fitted with sampling rods under the wing, calibrated at the start of each day to identify a 150 m observation strip on each side of the aeroplane when flying at 350 ft (109 m) above ground level. In addition to the pilot, each aeroplane contained a front seat observer with responsibility of announcing pre-georeferenced points (commonly referred to as subunits) to rear observers and recording the flying height and speed target of the aircraft. Two rear seat observers identify, count and record live elephants and elephant carcasses visible within the strip bounded by the distance rods on either side of the plane. In addition, they operated a camera set immediately by their head to record each wildlife observation and enable later checking of counts within the strip. Pilots aimed to fly at 109 m above ground level, at speeds of less than 180 km/h and along pre-defined transects 5 km apart. Strips were preferentially oriented North/South to improve light conditions for surveyors, but where landscape features favoured alternative alignments these were used: in two areas of the ecosystem regular ridge and valley systems were identified during the 2013 survey, so 450 km of transects were realigned to intersect the regular patterns in the landscape, otherwise transects were as similar as possible in each year (Fig. 1). Surveys were undertaken between 28 October and 7 November in 2013, 4 November

and 13 November in 2014 and 16 September and 13 October in 2015, at the height of the dry season when wildlife tends to be concentrated in open areas around rivers and trees are largely devoid of leaves improving visibility from the air. Only 7% of transect subunits were flown at average speeds in excess of 190 km/h and ~13% were flown at altitudes 15 m above or below target height, which we considered to have limited impact on overall results. We flew a total of 9125 km in 3650 subunits in 2013, 9707.5 km over 3883 subunits in 2014 and 9602.5 km in 3841 subunits during the 2015 survey. The high prevalence of both dense herds and single animals within the observed dataset renders abundance modelling within these sparse spatial data impractical, and consequently we sought to model the presence/absence of animals and carcasses in each transect subunit. From the GPS tracks and altitude records, we reconstructed the actual survey strips of each subunit, assuming observations occurred in a window starting 100 m from either side of the flight line in a rectangle 2.5 km long and of between 90 m and 150 m wide, depending on recorded altitude and flight specific calibration metrics.

### 2.3. Covariates

Factors that affect elephant distribution at fine scale are well known. Primary drivers are associated with food and water availability (Chamaillé-Jammes et al., 2007), with presence of humans an additional factor (Hoare and Du Toit, 1999). To incorporate information on the primary drivers of elephant distribution, we used variables derived from satellite data to estimate primary productivity and the availability of standing water in the landscape at both the height of the dry season and the middle of the wet season. To test hypotheses concerning tree cover, we estimated percent cover from remote sensing data. To test hypotheses concerning poaching, we calculated the travel cost of poachers from neighbouring villages to all points within the protected area (accounting for distance, terrain and physical boundaries such as large rivers and forests) and measured the distance to the nearest ranger post within the management unit. Additionally, within analyses of carcass density, we incorporated the estimated density of live elephants, expecting carcasses may be found in areas where elephants are common (Rashidi et al., 2015, 2016). We overlaid all covariate datasets with the transect subunit polygons and extracted the mean value for each covariate within the survey polygon.

We estimated woody vegetation cover using supervised classification of 30 m resolution corrected, cloud-free LandSat8 images made at the end of the wet season in 2015. Full details of tile identity and woody cover estimation are provided in supplementary methods.

We used the same LandSat8 tiles and initial correction to identify presence of water at 30 m resolution. To process wet season data we selected two largely cloud free images from February – April and for the dry season two images from August or September. Using bands 3 and 6, we calculated a modified normal difference water index following (Xu, 2006) and selected a threshold that reliably identified known seasonal and permanent waterholes separately for each image. To minimize residual cloud artefacts we selected only areas where both images independently classified pixels as water to generate a single final map for each season. We mosaiced individual tiles and aggregated to 500 m indicating presence/absence of water, before finally computing distance to water for all pixels.

We estimated the relative cost of travel from all villages to any pixel within the study area from the mapped road network (a custom-built dataset of roads within Ruaha NP driven by the project team, combined with roads in other areas digitized from Google Earth), the topographic roughness (from the ASTER GDEM 30 m, retrieved from https://lpdaac.usgs.gov), the position of major rivers (FAO, 2002) and the presence of forest in the most frequent land cover estimate over 12 years from the MODIS Land Cover data MDC12Q2 (Friedl et al., 2010). These surfaces were used to generate a combined travel cost from all villages surrounding the study area following Critchlow et al. (2015), who showed

significant correlations with travel cost and various illegal activities in a Ugandan National Park.

We identified management units from boundary data digitized by Wildlife Conservation Society staff and manually marked positions of ranger posts within Ruaha NP and the park head quarters of Rungwa GR with GPS. No permanent ranger posts exist elsewhere within the study area. For each management unit we identified the distance to and identity of the nearest ranger post within the management unit. We used the MODIS Net Primary Productivity MOD17A3H v6 product (Running et al., 2015) for estimates of food availability.

### 2.4. Data and analysis

We undertook all spatial analysis in R, using integrated nested Laplace approximation (implemented in the R-INLA package: (Lindgren and Rue, 2015). INLA provides a computationally efficient method for the analysis of complex hierarchical models: spatio-temporal analyses of thousands of rows of data are now achievable on desktop computers in reasonable time. For both live elephants and carcasses we built a series of spatially-explicit generalised additive models (GAM). To account for spatial autocorrelation in the residuals these models contain an intrinsic conditional autoregressive model (iCAR: Besag et al., 1991). For woody cover and the cost of travel for poachers, we considered a priori that non-linear relationships may be important and modelled these covariates with a GAM with two knots, restricting the fitted relationship to a monotonic or monomodal function. We modelled other variables as linear effects after centring and scaling to a standard deviation of one. We tested specific hypotheses about the distribution patterns of elephants within the protected area, assessing the support for alternative models using Watanabe-Akaike's Information Criteria (WAIC), the best performing Bayesian information criterion (Gelman et al., 2013). All models included fixed effects for NPP, altitude, woody cover, poacher cost, distance to water during both wet and dry season and their interactions with year (our 'full model'). All models of elephant carcasses additionally included the mean estimate of live elephant probabilities from the models for the respective survey year. Full details of the spatially explicit GAM model structure are provided in detail in Beale et al. (2014) and code for implementing the specific models is provided as supplementary material.

To test the hypothesis concerning changes in elephant and poacher behaviour between years, we fitted models without interactions between year and each covariate in turn and compared this to the full model. To test the hypothesis concerning carcass density in relation to ranger posts and management blocks we fitted additional models that included the interaction between distance to nearest ranger post within the management area and the identity of that ranger post, enabling a model of the effect of each individual post to be estimated. We compared these full models with models first without a year interaction and secondly without an interaction between ranger post identity and distance. If individual ranger posts show different performance (e.g. one post has a deterrent effect, but another less so) we expected greatest support for the models involving interactions between ranger post identify and distance. As ranger post identity is a factor, these models could only be fitted for zones where dead or living elephants were actually observed, and to ensure comparability we restricted the analysis to zones where both live and dead elephants were found (13 of a possible 21 ranger zones).

## 3. Results

### 3.1. Overall distributions

Elephants and their carcasses were widely distributed but aggregated across in all years, with more locations of carcasses than live elephants (Fig. 2). Highest densities of live elephants were along the Ruaha river in the south and east of the ecosystem, with additional concentrations in 2013 and 2015 in the western areas of Rungwa that were not so evident in 2014, when locations with live elephants were much scarcer (Fig. 2a-c). By contrast, the maps of carcasses suggest a large-scale change in the distribution of carcasses between 2013 and 2014, mostly driven by an increase in carcass density towards the centre of the ecosystem in the second two years (Fig. 2d-f).

### 3.2. Drivers of distribution

We found support for a small shift in live elephant distribution in relation to tree cover between the three surveys (model Fixed.tree showed a modest increase in WAIC with respect to the full model: Table 1), with elephants tending to prefer more open habitats and not to be located in dense areas of tree cover in 2014 where they were present in 2013 and 2015 (Fig. 3a). No other year interactions were well supported by the data (no other WAIC scores for interaction models exceeded 2: Table 1), but there was good support for main effects of distance to ranger stations (more elephants occurring closer to ranger stations: Fig. 3g) and for live elephants occurring in areas of intermediate travel cost from villages (Fig. 3e, all results from Table 1). Altogether, fixed effects excluding year explained a maximum of 67% of the variation in predicted values.

We found no support for temporal changes in spatial distribution of carcasses with respect to the covariates (no WAIC scores for interaction models exceeded 2: Table 2) and overall models of carcass distribution showed somewhat lower predictive power of the fixed effects (59% of variation) and concomitant increase in the importance of the spatial effect when compared to live elephants. In all years carcasses were most frequently encountered in areas of intermediate tree cover, lower altitudes, closer to wet season water sources, further from wet season water sources and in areas of intermediate travel cost from villages (Fig. 4). The models provided strong support for a negative effect of altitude and distance to wet season water sources (WAIC scores substantially higher in models without these effects: Table 2) and modest support for the effect of travel cost to villages (WAIC score of model No.cost 0.997 greater than null: Table 2). We found no evidence overall that distance to ranger post was correlated with carcass distribution nor that the probability of detecting live elephants was strongly correlated with carcass density (Table 2).

Our models that separated the management areas into zones patrolled by each ranger post (incorporated interactions between ranger post identity and distance) showed a more complex picture. For live elephants, we found most support for the model involving a three-way interaction between year, ranger post identity and distance (WAIC in this model 1700, for no year interaction 1770 and for no interaction between ranger post identity and distance 1721) suggesting a complex pattern of association or avoidance of individual ranger posts by live elephants (Fig. 5). For carcasses, we found highest support for the model with an interaction between ranger post identity and distance (WAIC 31 lower than full model, and 53 lower than model without the interaction), providing strong evidence that individual ranger posts have different effects on carcass occurrence (Fig. 5), from many posts with no strong influence (e.g. Fig. 5b, e & f), to a few where elephant carcasses were more likely to be found close to the ranger post (e.g. Fig. 5a, c & d) and a few having a clear negative effect on carcass density close to ranger posts, including the National Park headquarters at Msembe (Fig. 5l).

At Msembe, estimated encounter probabilities of carcasses were 0.006 within 5 km of the ranger post and 0.015 within 5–10 km. Across all ranger posts, the sum of probabilities (essentially the expected number of separate carcass encounters across all three survey years) within 5 km of any ranger post was 154.0, and between 5 and 10 km of any ranger post was 239.5. If all elephant death in the immediate vicinity of ranger posts were as low as around Msembe, the expected number of carcass encounters within 5 km of a ranger post would be 1.4, with a further 6.7 between 5 and 10 km, suggesting a total
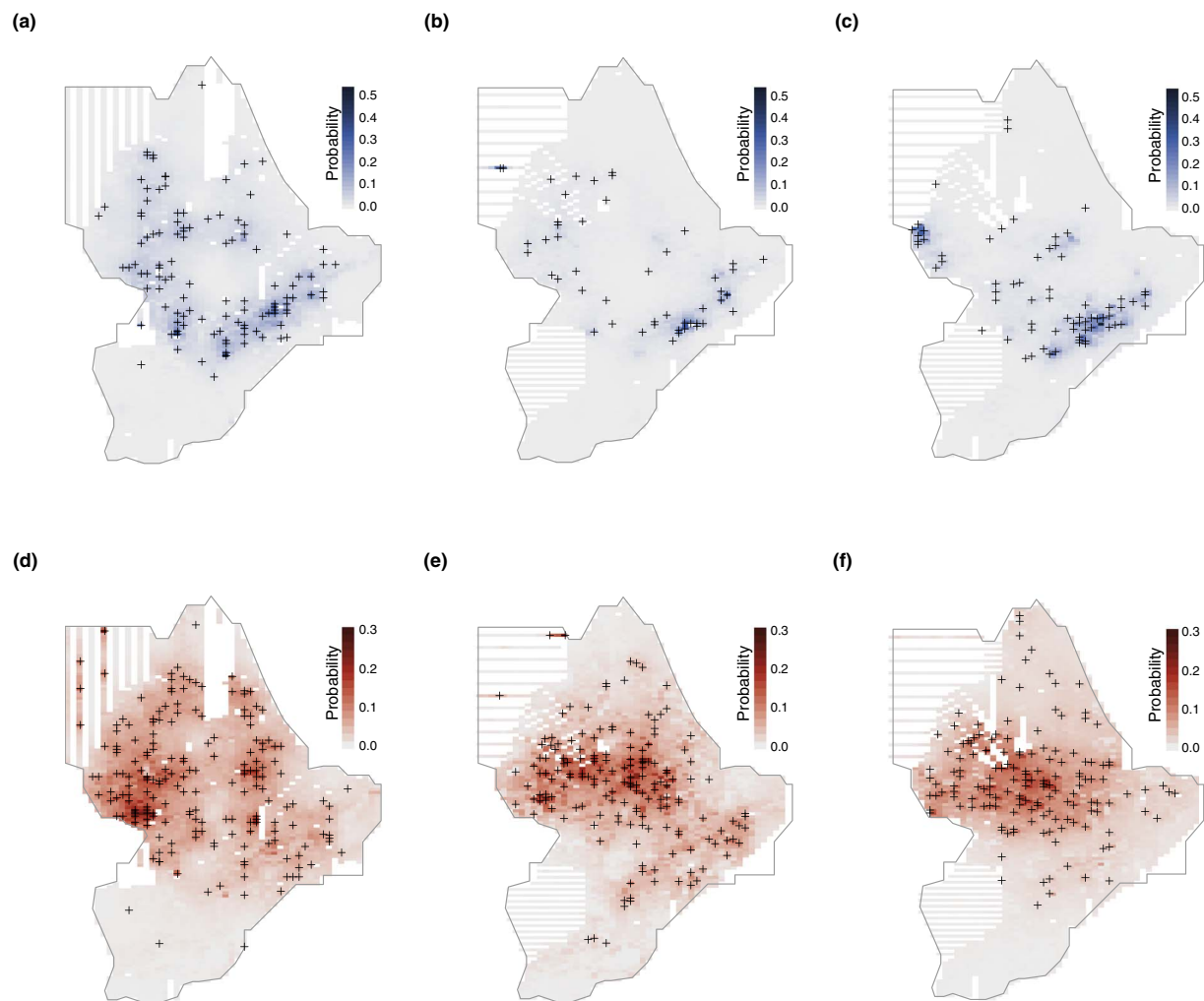
**Fig. 2.** Locations (crosses) and modelled probabilities (shading) of occurrence of live and dead elephants within the Ruaha-Rungwa Ecosystem. Top row shows results for live elephants (a) 2013, (b) 2014, (c) 2015, second row results for carcasses (d) 2013, (e) 2014, (f) 2015.

**Table 1**

WAIC scores for candidate models of live elephants. Bold figures indicate effects where Δ WAIC > 2, indicating strongly supported parameters.

| Model | WAIC | Δ WAIC | Description |
| --- | --- | --- | --- |
| Full | 1912.0 | | Full model with year interaction with all covariates |
| Fixed.tree | **1915.9** | **3.907** | Full model without tree cover × year interaction |
| Fixed.NPP | 1913.1 | 1.168 | Full model without NPP × year interaction |
| Fixed.dry | 1910.5 | − 1.443 | Full model without distance to dry season water × year interaction |
| Fixed.alt | 1910.4 | − 1.591 | Full model without altitude × year interaction |
| Fixed.wet | 1910.3 | − 1.684 | Full model without distance to wet season water × year interaction |
| Fixed.cost | 1910.0 | − 1.979 | Full model without poacher travel cost × year interaction |
| Fixed.ranger | 1909.6 | − 2.420 | Full model without distance to ranger station × year interaction |
| No.interactions | 1906.8 | − 5.138 | Model with all covariates but no year interactions |
| No.rangers | **1920.8** | **13.977** | Model with no year interactions and without distance to ranger station |
| No.cost | **1914.9** | **8.029** | Model with no year interactions and without poacher travel cost |
| No.wet | 1908.5 | 1.699 | Model with no year interactions and without distance to wet season water |
| No.dry | 1906.9 | 0.018 | model with no year interactions and without distance to dry season water |
| No.alt | 1906.7 | − 0.153 | Model with no year interactions and without altitude |
| No·NPP | 1906.6 | − 0.244 | Model with no year interactions and without NPP |
| No.tree | 1901.7 | − 5.192 | Model with no year interactions and without tree cover |
| No.year | **1916.4** | **9.586** | Model with no year effect at all |

reduction of 385.4 carcass encounters across the landscape, or 7% of the expected carcass encounters.

## 4. Discussion

We built informative models of the fine-scale distribution of both live and dead elephants using widely available aerial survey data, such as that generated by the "Great Elephant Census" (Chase et al., 2016). Our models identified carcasses spread widely across the ecosystem, with distributions of carcasses differing significantly from those of live elephants and changing from more peripheral areas in 2013 towards the core of the ecosystem in subsequent years. Live elephants remain
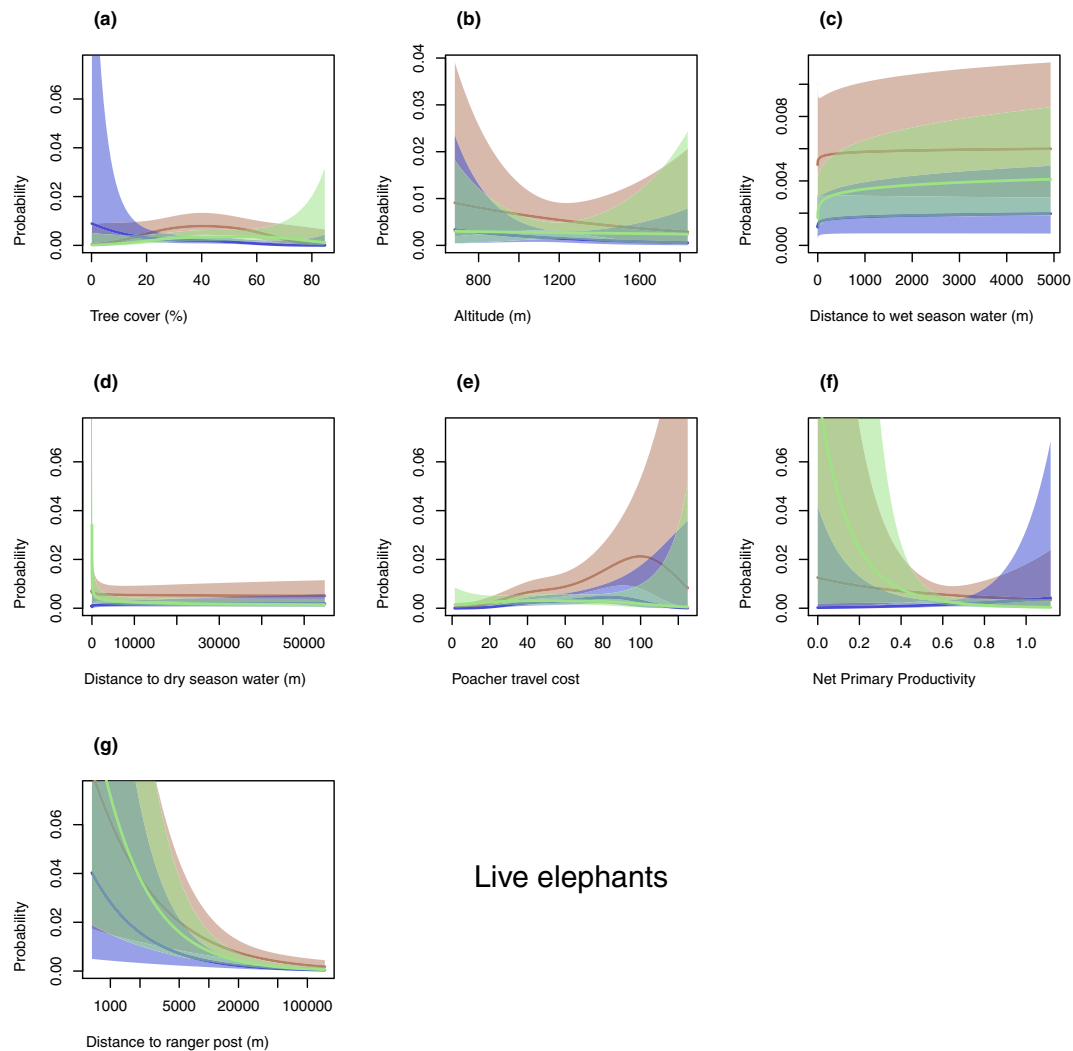
**Fig. 3.** Fixed effect plots for live elephants based on their distributions in 2013 (red), 2014 (blue) and 2015 (green) in the Ruaha-Rungwa ecosystem. Well supported differences between years were only found for tree cover (a). Additional support for main effects were present for distance to ranger post (g) and poacher travel cost (e). No strong support was found for effects of distance to wet season waterholes (c), distance to dry season waterholes (d) or net primary productivity (f). (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

**Table 2**
WAIC scores for candidate models of elephant carcasses. Bold figures indicate effects where Δ WAIC > 2 identifying strongly supported parameters.

| Model | WAIC | Δ WAIC | Description |
|---|---|---|---|
| Full | 3701.9 | | Full model with year interaction with all covariates |
| Fixed.alt | 3703.0 | 1.048 | Full model without altitude × year interaction |
| Fixed.live | 3702.6 | 0.695 | Full model without live density × year interaction |
| Fixed.NPP | 3702.0 | 0.053 | Full model without NPP × year interaction |
| Fixed.wet | 3702.0 | 0.043 | Full model without distance to wet season water × year interaction |
| Fixed.rangers | 3701.1 | − 0.822 | Full model without distance to ranger station × year interaction |
| Fixed.cost | 3699.5 | − 2.450 | Full model without poacher travel cost × year interaction |
| Fixed.dry | 3699.2 | − 2.695 | Full model without distance to dry season water × year interaction |
| Fixed.tree | 3695.9 | − 6.011 | Full model without tree cover × year interaction |
| No.interactions | 3693.1 | − 8.851 | Model with all covariates but no year interactions |
| No.alt | **3705.0** | **11.963** | Model with no year interactions and without altitude |
| No.wet | **3695.7** | **2.662** | Model with no year interactions and without distance to wet season water |
| No.cost | 3694.1 | 0.997 | Model with no year interactions and without poacher travel cost |
| No.dry | 3693.1 | 0.021 | Model with no year interactions and without distance to dry season water |
| No.rangers | 3692.5 | − 0.579 | Model with no year interactions and without distance to ranger station |
| No.live | 3691.2 | − 1.860 | Model with no year interactions and without live density |
| No.tree | 3690.9 | − 2.137 | Model with no year interactions and without tree cover |
| No·NPP | 3690.8 | − 2.264 | Model with no year interactions and without NPP |
| No.year | **3698.6** | **5.523** | Model with no year effect at all |
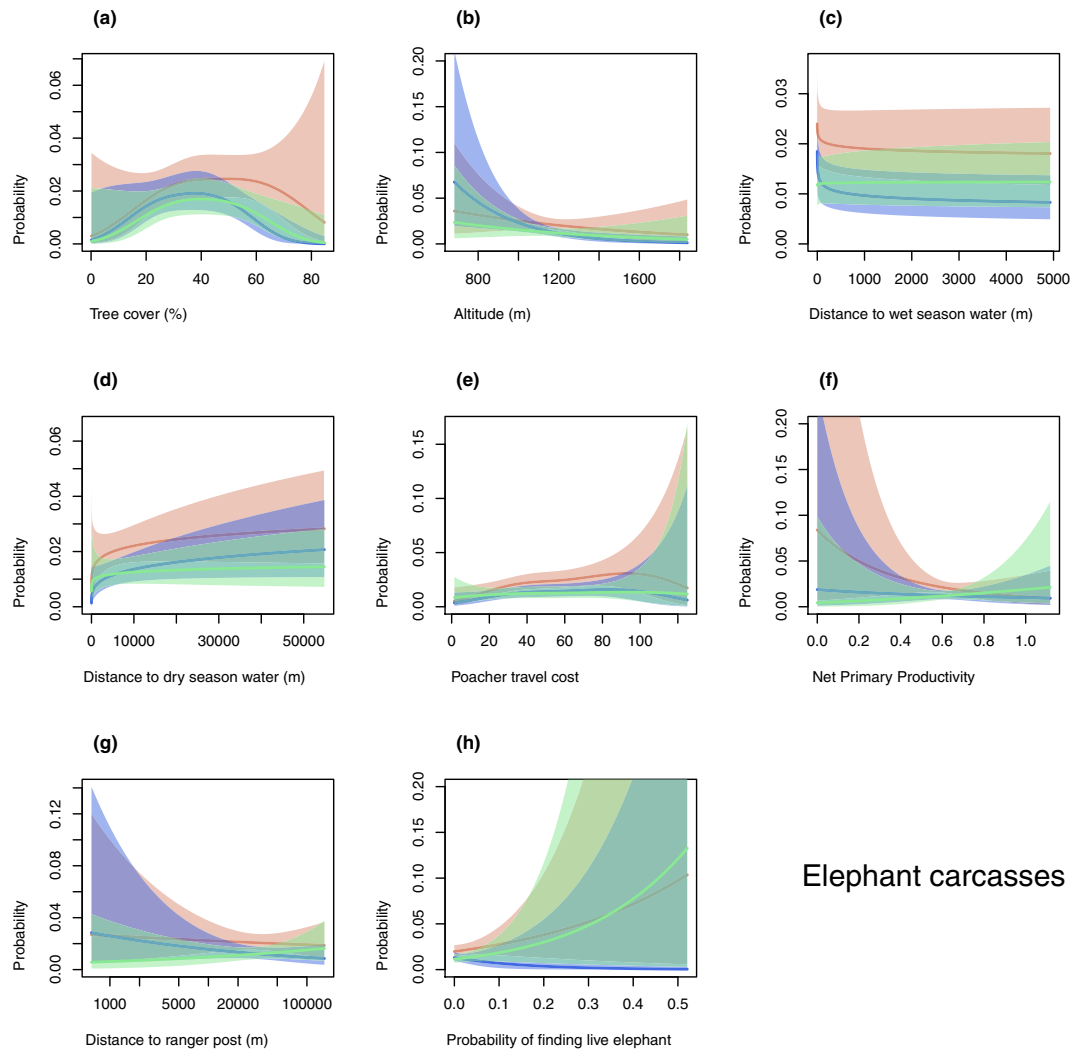
**Fig. 4.** Fixed effect plots for elephant carcasses based on their distributions in 2013 (red), 2014 (blue) and 2015 (green) in the Ruaha-Rungwa ecosystem. No strong support for difference between year, but altitude (b) and distance to wet season water holes (c) were correlated with overall patterns, and the travel cost to villages (e) had some support. No strong support was found for effects of distance to dry season waterholes (d), net primary productivity, (f) or live elephant occurrence (g). (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

widespread across the ecosystem, but we noted a shift in the distribution of live elephants in 2014, with an apparent disappearance from many of the intermediate density woodlands preferred in 2013 and 2015. This shift in distribution occurred at the same time as a major shift in carcass distribution and when the overall survey estimated a lower elephant population than either of the other two surveys (TAWIRI, 2014). Although the anomalous population estimate in 2014 is probably influenced by the chance non-detection of a few large herds, it may also be contributed to by one of two additional processes: a behavioural response by remaining elephants to the levels of poaching since the 2013 survey resulting in temporary emigration from the survey area, or decreased detectability of live elephants occupying woodland areas in 2014 due to different leaf cover(c.f. Ndaimani et al., 2016). Although leaf cover was not recorded and phenology of leaf burst in miombo woodlands can be variable (Chidumayo, 2001), the survey in 2014 was earlier than either 2013 or 2015 suggesting phenology should have been at a less advanced stage. We therefore suggest the low count in 2014 may be influenced both by undercounting and by temporary emigration.

Most patterns we find in relation to carcasses confirm earlier work or general expectations although we noted a mismatch between the locations of live elephants and the locations of carcasses. As has been the case for many years (Barnes, 1983), we found live elephants in

concentrations near the Ruaha river in the east of the survey area and over more widely scattered locations in the west, while carcasses were concentrated around the northern and western periphery of the survey area in 2013 before being located more commonly in the central areas in 2014 and 2015. Despite the obvious shift in locations of carcasses over time (captured in our models by changes in the spatial random effect rather than year interactions with fixed effects), our models suggested the underlying correlates of poaching patterns remained the same, and were similar to those reported elsewhere: more elephant carcasses occurred in the higher altitude western areas and in the areas closer to wet season waterholes, with some support for models including areas of intermediate travel cost from villages (c.f. Critchlow et al., 2015; Rashidi et al., 2015, 2016). Such information, and the maps generated by this type of analysis, can be used to increase the efficiency of ranger patrols, targeting effort to the highest priority areas (Critchlow et al., 2016). The rapid change in distribution of carcasses also suggests that the assumed carcass decay rate may be too low: if 50% of carcasses from 2013 were still visible in 2014 we would have seen a rather less dramatic shift of carcasses away from the peripheral areas where they were common in 2013. Carcass decay rates were originally estimated from very limited samples (Coe, 1978; Hanks and McIntosh, 1973) and it seems reasonable to expect some variation based on local carnivore/scavenger density and other environmental
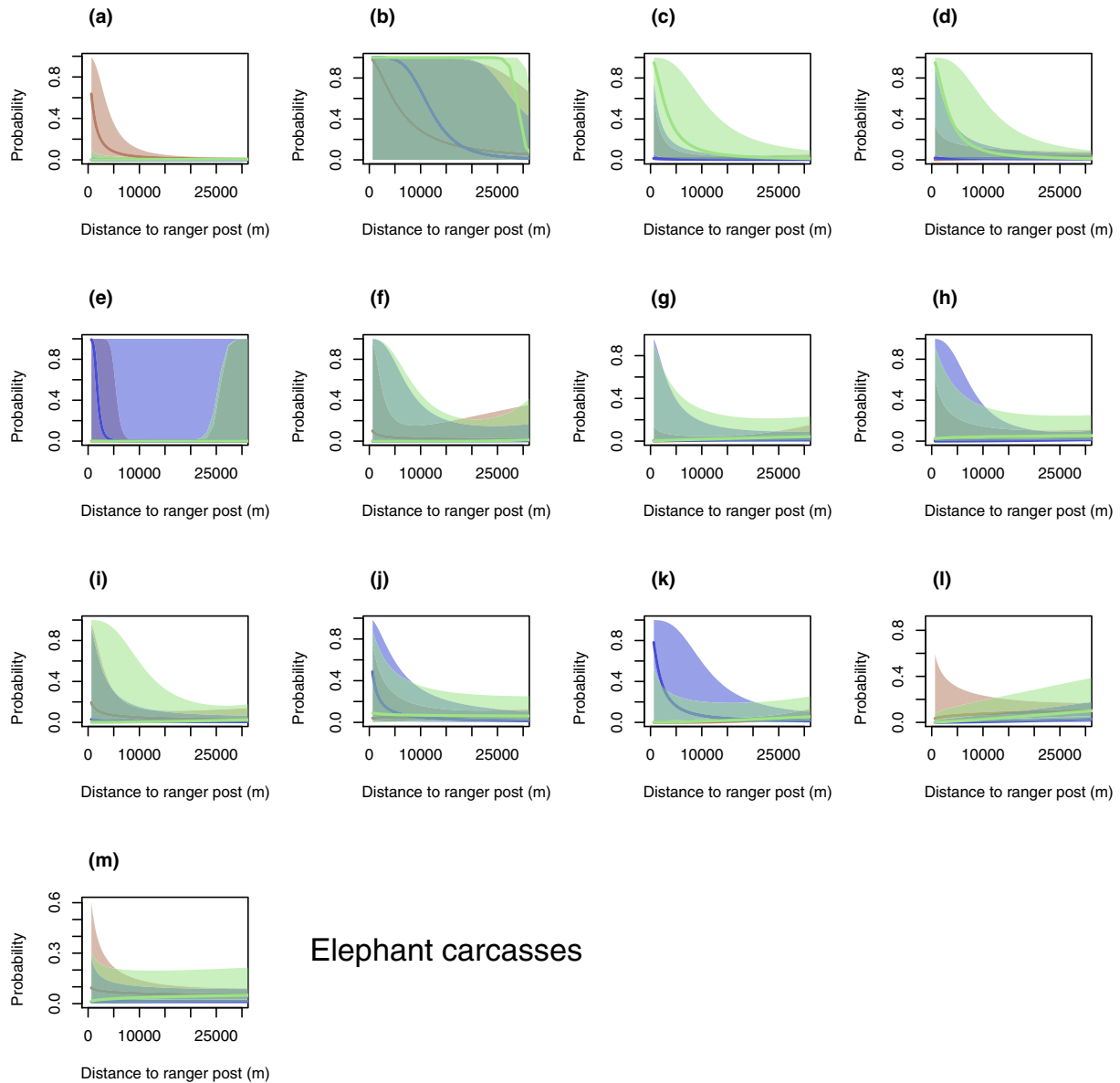
**Fig. 5.** Relationships between carcass occurrence and distance to each ranger post in 2013 (red), 2014 (blue) and 2015 (green) in the Ruaha-Rungwa ecosystem. Ranger posts are anonymised for presentation, but note that while the majority of points show no well supported patterns, there is evidence for carcasses occurring closer to posts (a), (c) and (d), and evidence that around Msembe (l) there are lower probabilities close to ranger posts. (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

factors (Wells, 1989): without local information on decay rates we suggest it is important not to overinterpret carcass ratios.

The observation that live elephant locations (surveyed during the dry season) and carcasses do not match well suggests an important result for managers: that most elephant poaching in Ruaha-Rungwa probably occurs during the wet season. We found that it is the distribution of wet season water points that correlate with carcass density, and the overall mismatch between live elephant distribution (censused during the dry season) and elephant carcasses both suggest seasonal patterns in poaching focussed on the wet season when elephants are more dispersed throughout the ecosystem. This pattern contrasts with that observed in Tsavo in Kenya (Maingi et al., 2012) where poaching was mainly observed in the dry season and the general lack of seasonality observed at Queen Elizabeth National Park in Uganda (Critchlow et al., 2015), but is supported by evidence from the nearby Selous Game Reserve (Kyando et al., 2017), suggesting that local factors are likely important in determining timing of poaching activity, even if similar spatial covariates determine location of poaching activity.

Increasing patrol activity during the wet season is a clear priority within the Ruaha-Rungwa ecosystem.

The importance of deterrent effects of rangers is a key question for reducing poaching, with recent work showing no apparent effects on rhino poaching (Barichievy et al., 2017) but others reporting deterrent effects on bushmeat poaching (Moore et al., 2017). Our analysis provides evidence that different ranger posts show different correlations with carcass distribution. In essence, our evidence suggests that whilst most ranger posts have no discernible impact on the distribution of carcasses, a small number such as the Ruaha National Park headquarters at Msembe are associated with fewer elephant carcasses in their immediate vicinity, whilst others seem associated with higher occurrence of carcasses. Variation in the numbers of carcasses in the areas around ranger posts could reflect both different resource allocation between posts and other activities associated with ranger posts. For example, Msembe, as park headquarters, is perhaps better resourced than other posts and is also at the centre of most tourism activities, probably providing additional deterrents to would-be poachers

([Laurance, 2013](#)).

Our results suggest that if elephant death were as low around all ranger posts as it is around Msembe (e.g. by hosting more, better resourced rangers and/or by increasing the tourism circuit), there could be an immediate reduction in elephant loss by 7% across the ecosystem. This is a relatively modest reduction in poaching, though none the less significant given the scale of the current problem. Moreover, this estimate is based on the distribution, not the numbers of carcasses and may therefore underestimate the effect of clustering. If deterrence is to increase, it is clear that there is a fundamental under-resourcing of rangers within the ecosystem. While IUCN guidelines advocate a rule of thumb law enforcement effort of one ranger for every 10–50 km$^2$ ([Henson et al., 2016](#)), when last censused, ranger densities in the study area varied from one per 140 km$^2$ within the National Park, to one per 346 km$^2$ in the game reserves ([Nahonyo, 2005](#)) and no effective patrolling in unprotected parts of the ecosystem. Although numbers of rangers have probably risen slightly since 2005, they are still well below the levels required to effectively protect elephants, but does suggest that despite evidence elsewhere, deterrence is possible even for high-value wildlife products with appropriate resource and training ([Barichievy et al., 2017](#)).

In summary, our analysis suggests that with a few exceptions where deterrence seems likely, widespread poaching across the Ruaha-Rungwa ecosystem is at best unaffected by proximity to ranger posts: poachers operate near waterholes where elephant activity is likely high and during the wet season when ranger patrols activity is minimal. To reduce poaching it is imperative to increase the efficiency of law enforcement by actively targeting the areas of highest poaching and by increasing activity during the wet season: our results suggest that at the best resourced ranger posts, and where tourism is high, deterrence has a measureable effect. This is an important positive message for law enforcement operations focussed on high-value wildlife. It is also essential to enhance ranger coverage overall by increasing both the numbers of rangers within the ecosystem and their effort in the field, especially on foot and coordinated with aerial surveillance in ecosystems with vast roadless areas such as Ruaha-Rungwa. Rangers in African parks can be extremely demoralised ([Ogunjinmi et al., 2008](#)), but better resourcing can lead to improved motivation and ultimately better performance ([Moreto et al., 2016](#)). Finally, we note that spatial analysis of widely available aerial survey data in combination with covariates collated in the field or from remote sensing offers a productive avenue for understanding fine-scale drivers of live animal distribution and insights into poacher activities across entire landscapes. Aerial survey data of elephants are widely available (e.g. the datasets from the Great Elephant Census: [Chase et al., 2016](#)), but spatial analysis should be applicable to any aerial survey datasets where geo-referenced data are routinely gathered, marine or terrestrial.

## Acknowledgements

## Appendix A. Supplementary methods

Supplementary data to this article can be found online at [https://doi.org/10.1016/j.biocon.2017.11.016](https://doi.org/10.1016/j.biocon.2017.11.016).

## References

Andriolo, A., Martins, C., Engel, M.H., Pizzorno, J.L., Más-Rosa, S., Freitas, A.C., Morete, M.E., Kinas, P.G., 2006. The first aerial survey to estimate abundance of humpback whales (*Megaptera movaeangliae*) in the breeding ground off Brazil (Breeding Stock A). J. Cetacean Res. Manag. 8, 307.

Barichievy, C., Munro, L., Clinning, G., Whittington-Jones, B., Masterson, G., 2017. Do armed field-rangers deter rhino poachers? An empirical analysis. Biol. Conserv. 209, 554–560.

Barnes, R.F.W., 1983. The elephant problem in Ruaha National Park, Tanzania. Biol. Conserv. 26, 127–148.

Beale, C.M., Brewer, M.J., Lennon, J.J., 2014. A new statistical framework for the quantification of covariate associations with species distributions. Methods Ecol. Evol. 5, 421–432.

Bennett, E.L., 2015. Legal ivory trade in a corrupt world and its impact on African elephant populations. Conserv. Biol. 29, 54–60.

Besag, J., York, J., Mollié, A., 1991. Bayesian image restoration, with two applications in spatial statistics. Ann. Inst. Stat. Math. 43, 1–20.

Booth, V.R., Dunham, K.M., 2016. Elephant poaching in Niassa reserve, Mozambique: population impact revealed by combined survey trends for live elephants and carcasses. Oryx 50, 94–103.

Challender, D.W.S., Harrop, S.R., MacMillan, D.C., 2015–2017. Understanding markets to conserve trade-threatened species in CITES. Biol. Conserv. 187, 249–259.

Chamaillé-Jammes, S., Valeix, M., Fritz, H., 2007. Managing heterogeneity in elephant distribution: interactions between elephant population density and surface-water availability. J. Appl. Ecol. 44, 625–633.

Chase, M.J., Schlossberg, S., Griffin, C.R., Bouché, P.J.C., Djene, S.W., Elkan, P.W., Ferreira, S., Grossman, F., Kohi, E.M., Landen, K., Omondi, P., Peltier, A., Selier, S.A.J., Sutcliffe, R., 2016. Continent-wide survey reveals massive decline in African savannah elephants. PeerJ 4, e2354.

Chidumayo, E.N., 2001. Climate and phenology of savanna vegetation in southern Africa. J. Veg. Sci. 12, 347–354.

CITES, 2016. Report on Monitoring the Illegal Killing of Elephants (MIKE) CoP17 Doc 57.5. CITES.

Coe, M., 1978. The decomposition of elephant carcasses in the Tsavo (East) National Park, Kenya. J. Arid Environ. 1, 71–86.

Critchlow, R., Plumptre, A.J., Driciru, M., Rwetsiba, A., Stokes, E.J., Tumwesigye, C., Wanyama, F., Beale, C.M., 2015. Spatiotemporal trends of illegal activities from ranger-collected data in a Ugandan national park. Conserv. Biol. 10, 572–580.

Critchlow, R., Plumptre, A.J., Alidria, B., Nsubuga, M., Driciru, M., Rwetsiba, A., Wanyama, F., Beale, C.M., 2016. Improving law-enforcement effectiveness and efficiency in protected areas using ranger-collected monitoring data. Conserv. Lett. http://dx.doi.org/10.1111/conl.12288.

FAO, 2002. Rivers of Tanzania - AFRICOVER.

Friedl, M.A., Sulla-Menashe, D., Tan, B., Schneider, A., Ramankutty, N., Sibley, A., Huang, X., 2010. MODIS collection 5 global land cover: algorithm refinements and characterization of new datasets. Remote Sens. Environ. 114, 168–182.

Gelman, A., Hwang, J., Vehtari, A., 2013. Understanding predictive information criteria for Bayesian models. Stat. Comput. 24, 997–1016.

Hanks, J., McIntosh, J.E.A., 1973. Population dynamics of the African elephant (*Loxodonta africana*). J. Zool. 169, 29–38.

Henson, D.W., Malpas, R.C., D'Udine, F., 2016. Wildlife Law Enforcement in Sub-Saharan African Protected Areas (No. Occasional Paper of the IUCN Species Survival Commission No. 58). IUCN.

Hoare, R.E., Du Toit, J.T., 1999. Coexistence between people and elephants in African savannas. Conserv. Biol. 13, 633–639.

IUCN, 2013. Elephant Database. URL. http://www.elephantdatabase.org/preview_report/2013_africa_final/2013/Africa, Accessed date: 22 December 2016.

Jones T, Cusack JJ, Pozo RA, Smit J, Mkuburo L, Baran P, Lobora AL, Mduma S & Foley C, in press Age structure as an indicator of poaching pressure: insights from rapid assessments of elephant populations across space and time. Ecol. Indic.

Kohi, E.M., de Boer, W.F., Peel, M.J.S., Slotow, R., van der Waal, C., Heitkönig, I.M.A., Skidmore, A., Prins, H.H.T., 2011. African elephants *Loxodonta africana* amplify browse heterogeneity in African savanna. Biotropica 43, 711–721.

Kyando, M., Ikanda, D., Røskaft, E., 2017. Hotspot elephant-poaching areas in the Eastern Selous Game Reserve, Tanzania. Afr. J. Ecol. 55, 365–371.

Laurance, W.F., 2013. Does research help to safeguard protected areas? Trends Ecol. Evol. 28, 261–266.

Laurance, W.F., Useche, D.C., Rendeiro, J., Kalka, M., Bradshaw, C.J.A., et al., 2012. Averting biodiversity collapse in tropical forest protected areas. Nature 489, 290–294.

Lindgren, F., Rue, H., 2015. Bayesian spatial modelling with R-INLA. J. Stat. Softw. 63 (25) web.

Maingi, J.K., Mukeka, J.M., Kyale, D.M., Muasya, R.M., 2012. Spatiotemporal patterns of elephant poaching in south-eastern Kenya. Wildl. Res. 39, 234–249.

MNRT, 2007. The Wildlife Policy of Tanzania Updated 2007.

Moore, J.F., Mulindahabi, F., Masozera, M.K., Nichols, J.D., Hines, J.E., Turikunkiko, E., Oli, M.K., 2017. Are ranger patrols effective in reducing poaching-related threats within protected areas? J. Appl. Ecol. http://dx.doi.org/10.1111/1365-2664.12965.

Moreto, W.D., Brunson, R.K., Braga, A.A., 2015. "Such misconducts don't make a good ranger": examining law enforcement ranger wrongdoing in Uganda. Br. J. Criminol. 55, 359–380.

Moreto, W.D., Lemieux, A.M., Nobles, M.R., 2016. "It's in my blood now": the satisfaction of rangers working in Queen Elizabeth National Park, Uganda. Oryx 1–9.

Nahonyo, C.L., 2005. Assessment of anti-poaching effort in Ruaha National Park, Tanzania. Tanzan. J. Sci. 31, 13–21.

NBS, 2012. The 2012 Population and Housing Census. URL. http://www.nbs.go.tz/nbstz/index.php/english/statistics-by-subject/population-and-housing-census/697-2012-phc-regional-profiles, Accessed date: 8 January 2016.

Ndaimani, H., Murwira, A., Masocha, M., Gara, T.W., Zengeya, F.M., 2016. Evaluating performance of aerial survey data in elephant habitat modelling. Afr. J. Ecol. http://dx.doi.org/10.1111/aje.12348.

Norton-Griffiths, M., 1978. Counting animals. In: Serengeti Ecological Monitoring Programme. African Wildlife Leadership Foundation.

Ogunjinmi, A.A., Umunna, M.O., Ogunjinmi, K.O., 2008. Factors affecting job satisfaction of rangers in Yankari game reserve, Bauchi, Nigeria. J. Agric. Soc. Res. 8. http://dx.doi.org/10.4314/jasr.v8i2.43332.

Ogutu, J.O., Piepho, H.-P., Said, M.Y., Ojwang, G.O., Njino, L.W., Kifugo, S.C., Wargute, P.W., 2016. Extreme wildlife declines and concurrent increase in livestock numbers in Kenya: what are the causes? PLoS One 11, e0163249.

Pimm, S.L., Jenkins, C.N., Abell, R., Brooks, T.M., Gittleman, J.L., Joppa, L.N., Raven, P.H., Roberts, C.M., Sexton, J.O., 2014. The biodiversity of species and their rates of extinction, distribution, and protection. Science 344, 1246752.

Rashidi, P., Wang, T., Skidmore, A., Vrieling, A., Darvishzadeh, R., Toxopeus, B., Ngene, S., Omondi, P., 2015. Spatial and spatiotemporal clustering methods for detecting elephant poaching hotspots. Ecol. Model. 297, 180–186.

Rashidi, P., Wang, T., Skidmore, A., Mehdipoor, H., Darvishzadeh, R., Ngene, S., Vrieling, A., Toxopeus, A.G., 2016. Elephant poaching risk assessed using spatial and non-spatial Bayesian models. Ecol. Model. 338, 60–68.

Rue, H., Martino, S., Chopin, N., 2009. Approximate Bayesian inference for latent Gaussian models by using integrated nested Laplace approximations. J. R. Stat. Soc. Ser. B Stat Methodol. 71, 319–392.

Running, S.W., Mu, Q., Zhao, M., 2015. MOD17A3H MODIS/Terra Net Primary Production Yearly L4 Global 500m SIN Grid V006. NASA EOSDIS Land Processes DAAC.

TAWIRI, 2013. Population Status of African Elephant in Ruaha –Rungwa Ecosystem, Dry Season, 2013. TAWIRI.

TAWIRI, 2014. Aerial Census of Elephant in the Ruaha-Rungwa Ecosystem, Dry Season, 2014. TAWIRI.

TAWIRI, 2015. Wildlife Survey in the Ruaha-Rungwa Ecosystem, Dry Season, 2015. TAWIRI.

Wasser, S.K., Brown, L., Mailand, C., Mondol, S., Clark, W., Laurie, C., Weir, B.S., 2015. Genetic assignment of large seizures of elephant ivory reveals Africa's major poaching hotspots. Science 349, 84–87.

Wells, M.P., 1989. The use of carcass data in the study and management of African elephants: a modelling approach. Afr. J. Ecol. 27, 95–110.

Wittemyer, G., Northrup, J.M., Blanc, J., Douglas-Hamilton, I., Omondi, P., Burnham, K.P., 2014. Illegal killing for ivory drives global decline in African elephants. Proc. Natl. Acad. Sci. U. S. A. 111, 13117–13121.

Xu, H., 2006. Modification of normalised difference water index (NDWI) to enhance open water features in remotely sensed imagery. Int. J. Remote Sens. 27, 3025–3033.