

RESEARCH ARTICLE

Staging behaviours identify spatial and temporal risk of human-wildlife conflict

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Award Number: 006784**Handling Editor:** Mahdiah Tourani**Abstract**

1. Habitat conversion to farmland has increased human-wildlife interactions, which often lead to conflict, injury or death for people and animals. Understanding the behavioural and landscape drivers of human-wildlife conflict is critical for managing wildlife populations. Staging behaviour prior to crop incursions has been described across multiple taxa and offers potential utility in managing conflict, but few quantitative assessments of staging have been undertaken. Animal movement data can provide valuable, fine-scale information on such behaviour with opportunities for application to real-time management for conflict prediction.
2. We developed an approach to assess the efficacy of six widely used metrics of animal movement to identify staging behaviour prior to agricultural incursions. We applied this approach to GPS data from 55 African elephants in the Serengeti-Mara ecosystem and found tortuosity and HMM-derived behavioural states to be the most effective for identifying staging events. We then assessed temporal patterns of defined staging at daily and seasonal scales and explored environmental and anthropogenic drivers of staging from spatial generalized logistic mixed models. Finally, we tested the viability of combining movement and simple spatial metrics to predict crop incursions based on GPS data.
3. Our approach identified staging behaviour that appeared to be driven largely by human activity and diurnal availability of protective cover from forest, riverine vegetation, and topography. Staging also varied substantially by season. Tortuosity and behavioural state metrics identified different staging strategies with distinct spatial distributions and anthropogenic drivers, and appeared to be linked to the juxtaposition between protected and cultivated lands. Tortuosity-based staging combined with distance-to-agriculture produced promising results for pre-event prediction of crop incursion.

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4. *Synthesis and applications.* Our study found staging by elephants prior to crop use could be identified from GPS tracking data, indicating that a better understanding of movement behaviour can inform targeted and proactive human-wildlife conflict management and inform spatial planning efforts. Our approach is extendable to other conflict-prone species to assess pre-conflict behaviours and space use and demonstrates some of the challenges and advantages of using animal behaviour to assess temporal and spatial heterogeneity in human-wildlife conflict.

KEYWORDS

African elephant (*Loxodonta africana*), biologging, GPS telemetry, human-wildlife interactions, movement ecology, space use, spatial risk, staging

1 | INTRODUCTION

Human expansion and habitat conversion in wildlife areas have increased the frequency of human-wildlife interactions, which can often lead to conflict, injury or death for people and animals (Woodroffe et al., 2005). Such negative interactions not only lead to direct losses, but can hamper wider conservation efforts and erode tolerance towards wildlife (Dickman, 2010; Goswami & Vasudev, 2017). Due to the expansion of conflict, understanding, predicting, and managing animal movements in human-dominated landscapes is a focus of conservation research (König et al., 2020). The spatial ecology of conflict, that is the spatial distribution of conflict and its behavioural and landscape drivers, can pinpoint risks and provide information to inform mitigation efforts (Bautista et al., 2021; Miller, 2015).

The spatial distribution of conflict is generally driven by the presence of humans and conflict resources, such as agriculture, water, or livestock (Broekhuis et al., 2017; Denninger-Snyder et al., 2019; Miller, 2015). However, given dynamics in resources and behaviour, risk of conflict is not static (Laffan et al., 2016). An animal's decision-making during conflict can be driven by risk-reward trade-offs akin to anti-predation behaviour (Frid & Dill, 2002), and this may result in spatial and temporal heterogeneity in conflict risk patterns as animals find movement strategies to adapt to a dynamic landscape and avoid people (Miller & Schmitz, 2019). Generally, locations of known conflict sites are used to assess and predict conflict risk (Bautista et al., 2021; Miller, 2015), but less is understood about space use leading up to conflict and how the landscape may facilitate or impede negative human-wildlife interactions (Blackwell et al., 2016). Identifying pre-conflict behaviour and understanding how temporal and spatial variation in this behaviour relates to conflict risk on the landscape could help elucidate trade-offs that animals make during crop incursions and inform how to manage landscapes to reduce conflict. Animal GPS telemetry can provide valuable and highly specific data to inform such assessments and also has the potential to be applied in real-time settings as an early warning system for negative human-wildlife interactions.

In many migratory species, staging and stopover sites provide a safe area to avoid predators while resting and refuelling during

migration (Dingle & Drake, 2007). The choice of stopover location and behaviour within these sites is generally the outcome of safety and foraging trade-offs, where animals may choose stopover sites with some food and little danger or seek out risky sites with access to food (Pomeroy et al., 2008). Characteristic pre-conflict movement behaviour, which we refer to as 'staging', that mimics this strategy has been described in multiple species including African and Asian elephants (Tiller et al., 2021; Wilson et al., 2015), American black bears (Marchinton, 1995), and monkeys (Mekonnen et al., 2012), although to our knowledge it has not been quantitatively defined and assessed. Across these species, staging behaviour is consistently described as embedded movement within densely covered habitat during the day in advance of incursions into crops and urban areas at night. Similar to choice of migratory stopovers, it is theorized that the areas used for staging are associated with refuge habitat that provides safety in human-dominated areas and allows animals to remain closer to high-quality food sources that require minimal travel and search time to obtain, despite these areas being more dangerous (Tiller et al., 2021).

Crop raiding by elephants is one of the most prevalent types of human-wildlife conflict in Africa and Asia, and is increasing with the spread of farms into wildlife range areas (Shaffer et al., 2019). As a result, local communities can incur substantial costs from elephants that damage crops and property, sometimes cause human injury or loss of life, and lead to retaliation killings of elephants (Denninger-Snyder et al., 2019; Shaffer et al., 2019). Elephants typically crop-raid at night when they are less likely to be detected (Sitati & Walpole, 2005; Tiller et al., 2021; Troup et al., 2020), and managers and communities employ a range of mitigations including flashlights, noisemakers, vehicles and firecrackers that can be difficult or dangerous to use at night (Shaffer et al., 2019). Elephants may also alter their normal activity budgets by reducing movement during the day and moving quickly through fields at night in order to access crops (Hahn et al., 2021). Conflict risk fluctuates annually, and in savannah systems, it is often linked to rainfall patterns as crops are primarily rain-fed and begin to mature as natural vegetation begins to desiccate (Branco et al., 2019). Spatially, crop raiding tends to occur more frequently closer to forest edges and protected areas and with lower human footprint (Denninger-Snyder et al., 2019;

Sitati & Walpole, 2005; Wilson et al., 2015). Elephants may also use these forest patches as staging areas to access crop fields (Tiller et al., 2021). Despite recognition of this behaviour and the potential utility of staging area identification for conflict mitigation, to our knowledge there have been no quantitative assessments of staging related to human-wildlife conflict for elephants or other species.

We analysed a long-term GPS elephant movement dataset to investigate the mechanisms and propensity of agricultural staging behaviour employed during crop raiding by elephants following four objectives. First, we outline and implement an approach to define agricultural staging (characteristic movements marked by low mobility during the day prior to night agricultural use) using six metrics derived from GPS movement data. Second, we evaluate and compare spatial drivers of staging clusters in relation to agriculture, protective cover vegetation, topography, and human footprint. Third, we assess how staging fluctuates temporally at daily and seasonal scales. Finally, we test the feasibility of using GPS-derived movement metrics and environmental parameters to predict night-time crop incursions from day-time movement data. We discuss our findings in the context of possible mechanisms driving staging behaviour, the implications for proactive management of human-wildlife conflict across species, and directions for future research.

2 | MATERIALS AND METHODS

2.1 | Study area

The study took place in the Serengeti-Mara Ecosystem, a savannah ecosystem in southwestern Kenya and northwestern Tanzania that covers over 40,000 km². The core area of the system is formed by the Serengeti National Park in Tanzania and the Masai Mara National Reserve in Kenya (38% of study area). It is bordered by limited use areas made up of community-managed conservancies with managed livestock grazing and no farming (14%). The remaining area is unprotected, comprised of private and community land used for crops and pastoralism (48%). Agriculture is primarily maize and other grain crops that have two growing seasons corresponding to the system's biannual rainfall pattern. The agricultural-protected interface ranges from a hard edge (non-protected crop land adjacent to core areas) to soft edges (limited use areas and forest patches providing a buffer between crop land and core areas). Human-elephant conflict fluctuates with crop cycles and is highest in the dry season, but incidences have risen overall in conjunction with agricultural expansion (Denninger-Snyder et al., 2019; Mukeka et al., 2019).

2.2 | Tracking data

We analysed GPS data collected from 2011 to 2021 from 59 elephants (205 elephant-years, average tracking time of 880 days) that have been tracked as part of long-term research projects in Kenya and Tanzania. Collaring ethical review was approved by the Colorado

State University IACUC committee (protocol no. 18-7744A and 19-9431A) and followed following procedures established by the Kenya Wildlife Service and Tanzania Wildlife Research Institute (dataset details in Hahn et al., 2021). GPS data was transmitted hourly via satellite. GPS data collected from females ($n=29$) represent a family unit while males ($n=30$) are dispersed and represent a single individual. Locations were filtered to the spatial extent of the study area, subsampled to 1-h intervals where necessary, and individuals with <95% fix success rates were removed. After cleaning, the dataset totalled 1,128,373 locations from 55 elephants. To delineate movement during agricultural use, we classified each day as agricultural use or non-use, based on whether an elephant was relocated in agriculture. Because agricultural use occurs primarily at night, a day was defined to start at 6 AM to avoid splitting an agricultural use event. There were 16,155 agricultural use days in the dataset.

2.3 | Environmental data

Spatial covariates were compiled to analyse agricultural use and staging locations (Table S2). Agriculture (8% of study area) was derived from a 30-m Landsat land cover classification of the Serengeti-Mara ecosystem published in Veldhuis et al., 2019. Forest cover (1% of study area) was determined from the 30-m Landsat forest cover change product in Google Earth Engine using 30% canopy cover in 2019 (Hansen et al., 2013). Normalized difference vegetation index (NDVI) was extracted from the 250m Moderate Resolution Imaging Spectroradiometer (MODIS) vegetation product from 2011–2021 at 16-day intervals and used to delineate wet, transition, and dry periods using Gaussian mixture clustering (Bastille-Rousseau et al., 2020). To delineate areas where water was readily available we extracted and buffered rivers and drainages from the global HydroSHED Free Flowing Rivers Network (Grill et al., 2019) by 250m corresponding to the mean step length for elephants. Slope was calculated based on the 30-m SRTM digital elevation model (Farr et al., 2007). Human footprint was assessed using the Google Open Buildings product for Africa (Sirko et al., 2021). Land use status was categorized as protected, limited use and unprotected (Figure 1).

2.4 | Agricultural staging identification

To address our first objective to identify agricultural staging behaviour, defined as pre-emptive day-time movement behaviour associated with agricultural use that evening, we used an unsupervised ensemble modelling approach to compare the efficacy of six different movement metrics to detect staging movement patterns: hourly step length, straightness index, tortuosity, net squared displacement, persistence velocity and percentage of encamped behaviour derived from hidden Markov models (previously derived in three-state HMM from Hahn et al., 2021; Table 1). We chose these metrics because they have either been found to capture differentiated movement behaviour in elephants during crop incursions (Hahn

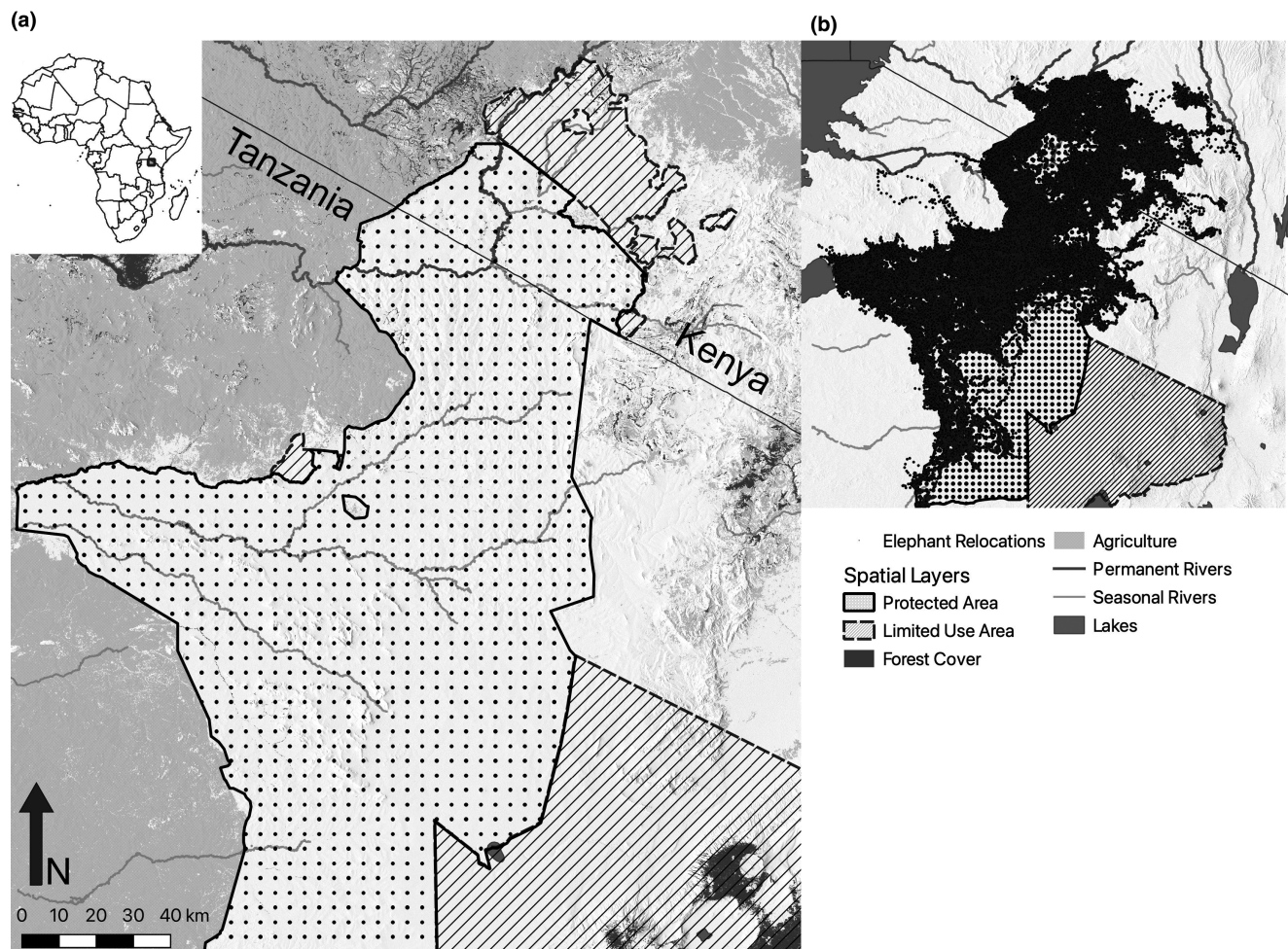


FIGURE 1 (a) The Greater Serengeti-Mara Ecosystem in Africa, showing protected and limited use areas, agriculture, forest, permanent and seasonal rivers, and topography. Areas not within protected and limited use boundaries are unprotected. (b) Shows the GPS relocations of the 55 individuals included in the study.

et al., 2021; Troup et al., 2020) or were expected to capture embedded movement consistent with previously observed staging behaviour (Seidel et al., 2018). Due to the correlation between metrics, we evaluated each separately using the same approach to identify the metrics with the greatest value for capturing staging.

Based on elephant activity budgets and timing of known agricultural use (Hahn et al., 2021; Tiller et al., 2021), we assumed a staging event could occur any time between 6 AM and 9 PM on a given day (stage time) and last anywhere from 2 to 15 h (stage length). To classify staging within these possible time windows, we used a threshold value for each movement metric, equal or above which a staging event was assigned, and tested a range of possible threshold values. The range of threshold values was based on the 75th or 25th percentile of a given movement metric's mean daily values, depending on the expected relationship of the metric with staging (Table 1). A detailed description of how movement metrics and threshold values ranges were calculated is reported in Appendix S1.

We classified agricultural staging events for each possible combination of stage time, stage length, and movement metric threshold value (Figure S1, example code in Appendix S3). We defined a true

positive as a detected staging event followed by agricultural use, a true negative as a non-staging event not followed by agricultural use, a false positive as a detected staging event not followed by agricultural use, and a false negative as a non-staging event followed by agricultural use. The efficacy of each parameter combination was evaluated using the positive predictive rate and the negative predictive rate (Equation 1), where FP is the number of false positives, TP is the number of true positives, FN is the number of false negatives, and TN is the number of true negatives for combination j . The positive predictive rate is the probability that a detected staging event does precede agricultural use. The negative predictive rate is the probability that agricultural use did not occur after a detected non-staging event,

$$\begin{aligned} \text{Positive predictive value}_j &= 1 - \frac{FP_j}{FP_j + TP_j}, \\ \text{Negative predictive value}_j &= 1 - \frac{FN_j}{FN_j + TN_j}. \end{aligned} \quad (1)$$

To consolidate a staging classification based on all parameter combinations, we used weighted majority voting (Punera & Ghosh, 2008)

TABLE 1 The movement metrics tested to define staging behaviour. Complete descriptions for the calculation and parameter space of each metric can be found in the [Supporting Information](#).

Metric	Definition	Expected relationship to staging	Reference
Mean step length	The mean displacement within the time window	Lower	Seidel et al. (2018)
Straightness index	The ratio of net displacement R to path segment length L ; $\log(R/L)$	Lower	Benhamou (2004)
Tortuosity	The ratio of path segment length L to net squared displacement R^2 ; $\log(L/R^2)$	Higher	Whittington et al. (2004)
Net squared displacement	The straight-line distance between the start and end of the trajectory	Lower	Seidel et al. (2018)
Persistence velocity	The mean of the speed of movement in the direction of heading; $\text{speed} \times \cos(\text{absolute turning angle})$	Lower	Seidel et al. (2018)
Encamped HMM behavioural state	Percentage of encamped GPS fixes from HMM model. HMM model used speed, turning angle and environmental covariates to estimate three behavioural states	Higher	Hahn et al. (2021)

Abbreviation: HMM, hidden Markov model.

to create an ensemble classification of staging for each movement metric. We assumed that elephants may not always stage before agricultural use, so we only used the positive predictive value (PPV) for weighting. For each combination j , weight w was assigned as the PPV to each GPS location i of a staging event (i.e. better prediction receives a higher weight) and as 0 for non-staging GPS locations. The weighted vote value v for each GPS location was calculated as the sum of weights across all j combinations (Equation 2; example code in Appendix S4):

$$v_i = \sum w_{ij}. \quad (2)$$

The GPS location was classified as a stage if the vote value was greater than the mean vote value for all locations to produce the ensemble classification (Equation 3; Figure S1). This was performed separately for each movement metric,

$$\text{Ensemble stage if } v_i > \frac{\sum v_i}{N}. \quad (3)$$

The efficacy of the ensemble classification for each movement metric was evaluated using the PPV and the negative predictive value (NPV; Equation 1).

2.5 | Spatial and temporal drivers of staging

To investigate our second objective, we assessed how agricultural staging events on the landscape were driven by natural and anthropogenic factors. To assess spatial drivers of agricultural staging, we used true positive staging events (i.e. only staging events on agricultural use days) and conducted separate analyses for each metric. The proportion of staging locations to total locations during agricultural use days were calculated on a 250m grid corresponding to mean hourly step length (Figure 2c). Environmental covariates were down-sampled and extracted for every grid cell. We used mixed-effects logistic regression with elephant ID as a random effect to assess the propensity to stage, where each cell value was weighted using the total count of locations for that cell. To account for spatial autocorrelation, we included an autocovariate based on an inverse weighting scheme, a symmetric neighbourhood matrix and a search radius that was defined dynamically for each elephant grid to select the lowest value at which all points had neighbours (Bardos et al., 2015). We developed biologically realistic candidate models and evaluated all models using corrected Akaike information criterion (AICc) (Burnham et al., 2011). Covariates (percent forest cover, percent agriculture, drainages, slope and percent permanent buildings) were

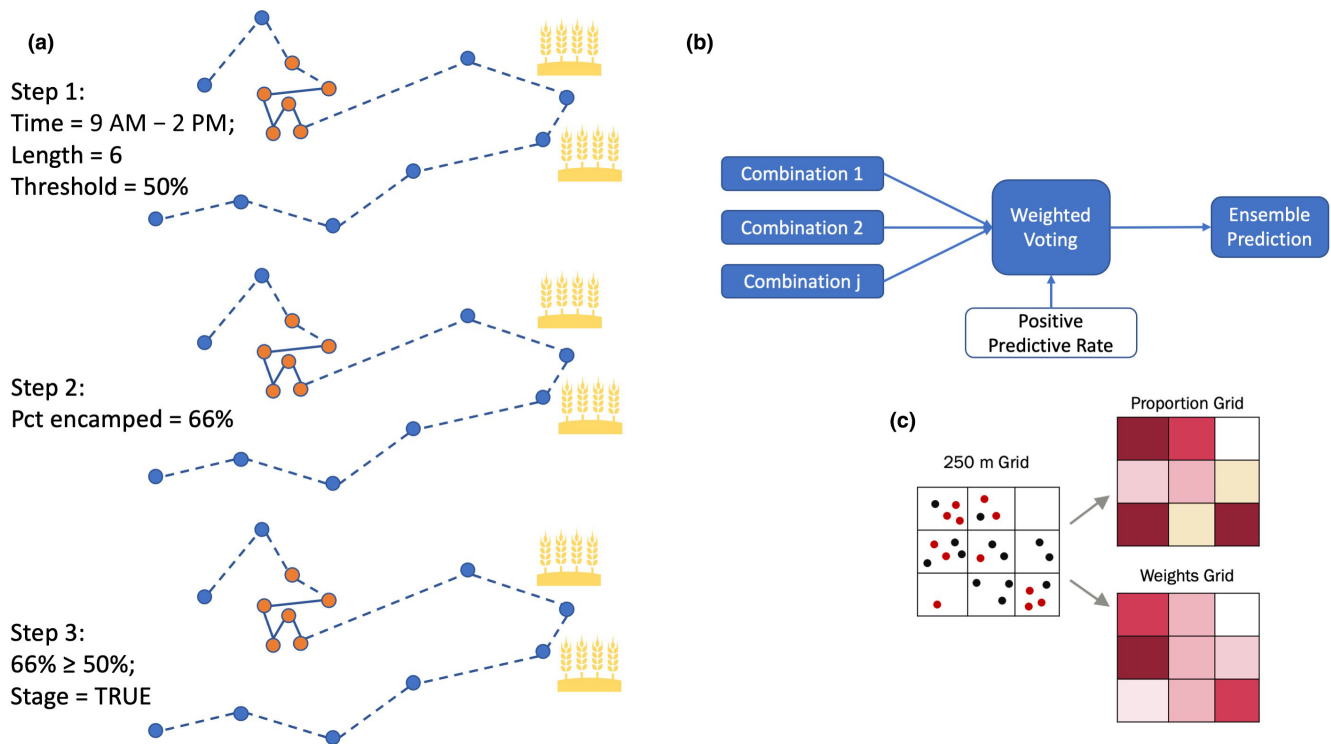


FIGURE 2 The analysis workflow for classification and spatial modelling of staging events from GPS data for encamped HMM-derived staging. (a) The sequence for testing a single combination of stage time, stage length and movement metric threshold value using an example movement trajectory. First the focal GPS locations are identified using time of day and stage length (orange dots) and the threshold movement metric is set; Second, the metric value is calculated for the focal locations (66% are encamped); Third this value is compared to the threshold metric and classified as a stage. (b) The results of each parameter combination are combined using weighted voting to produce an ensemble classification of staging events. (c) The GPS locations (dots) from true positive staging events are used to create a proportional and weights grid to model occurrence of staging in relation to environmental variables using weighted spatial regression. HMM, hidden Markov model.

chosen based on expectations that staging would relate to natural features which provide cover, agriculture and reduced exposure to human settlements. Because covariate values were measured at different scales, continuous covariates were scaled and centred. Tests for multicollinearity in predictors showed that variance inflation values did not exceed 1.5.

For our third objective, we investigated the timing of staging behaviour at daily and seasonal scales. At the daily scale, we assessed staging movement patterns by calculating the mean value of each movement metric and mean speed at each hour of the day for (1) agricultural use days with a stage, (2) agricultural use days without a stage, and (3) non-agricultural use days. At the seasonal scale, we calculated the percentage of agricultural use days with a stage occurring within wet, transition and dry seasons. To account for individual variation, we calculated staging percentages for each elephant-year.

2.6 | Enhancing predictive performance of staging

To address our fourth objective to assess the viability of predicting crop incursions, we compared our results using only stage time, stage length and movement (movement-only approach) to a second

approach that also incorporated spatial information on distance to agricultural (movement-agriculture approach). Such spatial filters that can remove biologically implausible stages (i.e. false-positive locations far away from crops) may be useful for improving prediction. We added a spatial threshold to mask out possible staging events based on the distance of a GPS location to agriculture. To limit false negatives, this spatial threshold was defined conservatively as the 95th percentile of Euclidean distance to agriculture during agricultural use days. We used PPV and NPV (Equation 1) to compare the movement-only and movement-agriculture results and evaluated the number of event triggers that would be missed and falsely triggered in a conflict prediction scenario as a yearly average.

3 | RESULTS

3.1 | Staging classification

In our evaluation of ensemble performance for staging classification, results varied between all metrics but we found that tortuosity and HMM-derived behavioural state were the most informative in relation to our objectives to predict agricultural use and investigate

spatial drivers of staging (see also all metrics, [Table S1](#)). Tortuosity produced the best NPV—87% with an interquartile range of 86%–91% between individuals—but performed worse with false positive errors—51% PPV, with IQR of 42%–53% ([Table 1](#)). Behavioural state had a worse NPV (36%, IQR of 29%–39%) but was better with PPV (56%, IQR of 56%–58%; [Table 1](#)). Ensemble classification of staging using tortuosity produced 13,954 true positive staging events occurring from 9 AM to 6 PM, with a mean of 83 stages per individual per year and 95% CI of 73–92. Classification of staging using behavioural state produced 5928 staging events occurring between 8 AM to 5 PM, with a mean of 30 stages per individual per year and 95% CI of 25–35. Movement patterns for agricultural staging were clearly differentiated between 8 AM and 6 PM ([Figures 4 and 5](#)), indicating our assumption to only consider 6 AM to 9 PM for staging events was valid.

3.2 | Spatial drivers of staging

For our second objective, we evaluated landscape properties of identified staging event locations ([Figure 3a,b](#)). For both staging definitions (tortuosity and behavioural state), the most parsimonious generalized logistic mixed model based on corrected Akaike information criterion (AICc) included proportion of forest cover, slope, drainages, proportion of agriculture and proportion of human settlement ([Tables S2 and S3](#)). The effect size for the proportion of forest cover covariate was the greatest for both tortuosity and behavioural state models, indicating strong selection for forest cover when staging ([Table 2](#)). Drainages also had a positive effect in both models. Behavioural state-defined staging was more positively correlated with proportion of agriculture, proportion of human settlement, and slope ([Table 2](#)). Tortuosity-defined staging was more likely to occur in protected and limited use areas compared to unprotected areas, while behavioural state-defined staging was most likely to occur in unprotected areas. Additionally, the autocovariate estimate for the behavioural state model was higher, indicating that it is more spatially clustered on the landscape. Tortuosity-defined staging appeared to occur predominantly in the Serengeti side of the system, while behavioural state-defined staging occurred more in the Mara ([Figure 3c,d](#); [Appendix S2](#), [Interactive Map](#)). In areas with high staging propensity (>50% of locations in a 250 m pixel related to staging events), tortuosity staging occurred across a greater area (1209 km²) relative to the area covered by behavioural state staging (307 km²; [Figure S4](#)).

3.3 | Temporal drivers of staging

At the daily scale, elephant movement metrics during agricultural use days showed strong differentiation when staging versus not during the day ([Figure 4a,b](#)). However, assessment of elephant speed during staging revealed that tortuosity staging averaged faster movements during the day than behavioural state staging ([Figure 5](#)). For both

metrics, stage length had a mean of 5 h with IQR of 3–7 h across individuals. At seasonal scales, tortuosity and behavioural state staging occurred more frequently during the transition and dry seasons, although staging also occurred during the wet season ([Figure S2](#)).

3.4 | Updating staging identification with spatial filters

We added a spatial threshold filter of 3.5 km for distance to agriculture (95th percentile) to remove possible staging events far from farms. This threshold improved PPVs across both movement metrics. The effect was most pronounced for tortuosity—PPV of 70%, an increase of 19% compared to the movement-only results. HMM-defined behavioural state also improved (65% PPV, increase of 9%; [Table 3](#)). NPVs for both metrics decreased with the spatial filter as it excluded true stages occurring more than 3.5 km from agriculture. Overall, tortuosity had the best balance between negative and PPVs of all 6 metrics after adding a spatial threshold for distance to agriculture ([Table S1](#)). In a conflict prediction scenario, using tortuosity and distance to agriculture would produce an average of 1741 total alarms per year with 522 false alarms and 250 missed alarms, while using encamped behavioural state and distance to agriculture would produce 813 total alarms per year including 284 false alarms, but 940 missed alarms.

4 | DISCUSSION

Crop raiding is one of the most prevalent types of human-wildlife conflict in Africa and Asia and has increased sharply with the spread of farms into wildlife range areas (Mukenka et al., 2019; Shaffer et al., 2019). Evaluation of spatial and temporal heterogeneity in conflict risk is critical to design conflict management plans (Laffan et al., 2016), but approaches that consider animal behaviour and space use leading up to conflict are limited (Blackwell et al., 2016). Staging behaviour prior to conflict has been described across multiple taxa and offers potential utility in managing and predicting conflict, but few quantitative assessments of staging have been undertaken. We developed approaches to identify staging behaviour prior to agricultural use from GPS tracking data using African elephants and six movement metrics (tortuosity and HMM-derived behavioural states being the most explanatory) as a case study. These metrics highlighted different aspects of staging behaviour that, ultimately, may be useful in addressing different objectives for managing human-elephant interactions. Specifically, the behavioural states application highlighted spatially constrained embedded staging events described elsewhere (Tiller et al., 2021), while tortuosity-based staging captured a spatially dispersed meandering staging behaviour that occurred more within protected areas. In contrast to our assumption of staging being highly embedded, tortuosity-based staging occurred more often and was more wide-spread in the study system.

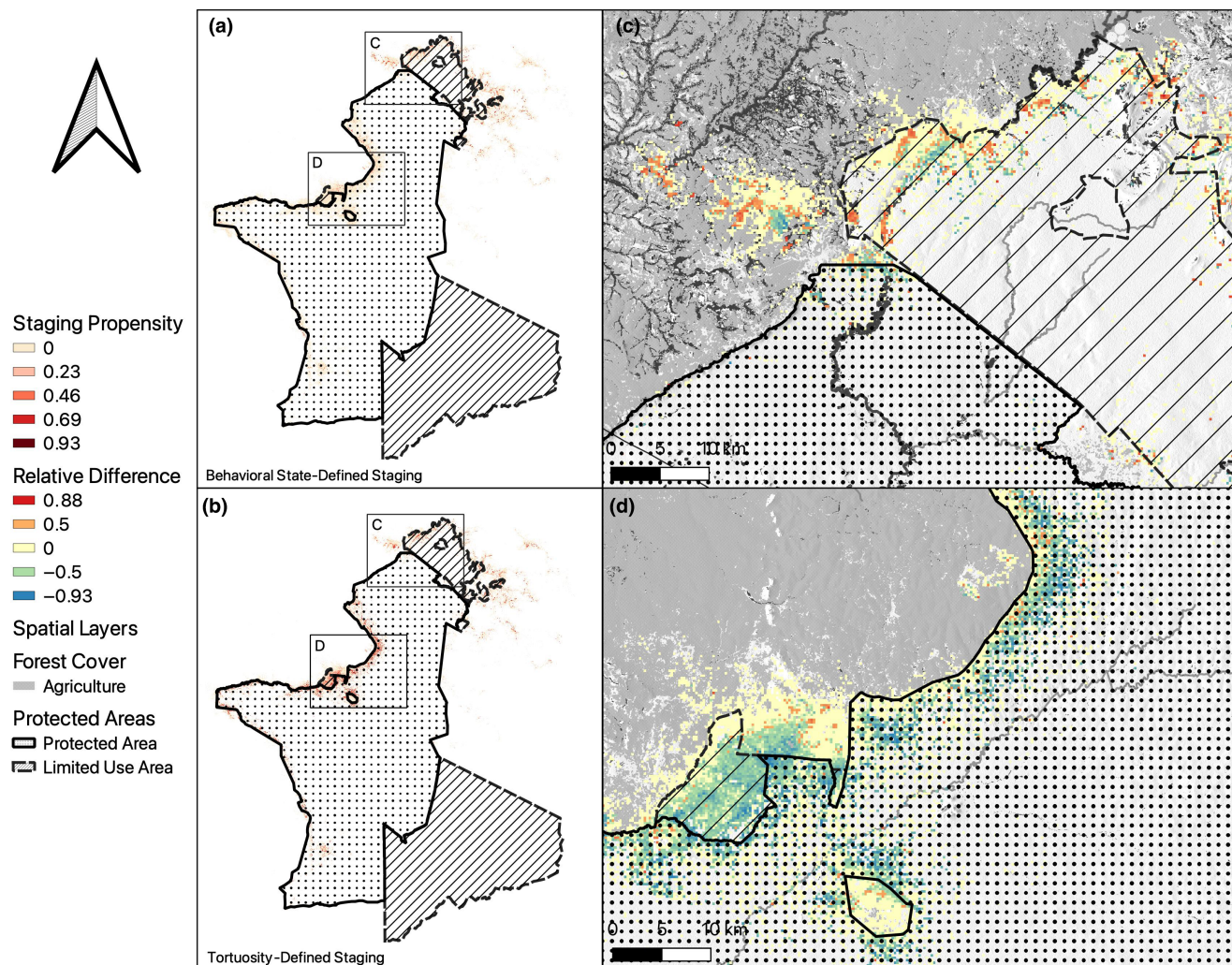


FIGURE 3 A comparison of the proportion of staging on the landscape produced by tortuosity and behavioural state staging definitions in the Serengeti-Mara System. Panels (a) and (b) show encamped behavioural state and tortuosity-defined staging propensity values, respectively. Darker reds indicate areas of greater staging propensity. Panels (c) and (d) show the relative difference in proportion values between tortuosity and behavioural state staging in the Mara (c) and Serengeti (d). Warmer colours (positive values) indicate cells with more behavioural state staging and cooler colours (negative values) indicate cells with more tortuosity-based staging. Areas of the map with no value indicate areas that elephants did not use during agricultural use days or that are in agriculture.

Our results highlight considerable heterogeneity in both the level and type of conflict risk and the ability of elephants to adapt their movement strategies depending on the landscape. To our knowledge, this was the first attempt to systematically identify staging behaviour related to human-wildlife conflict. Overall, the behavioural state-defined encamped staging occurred on a smaller subset of agricultural use days, but was highly spatially clustered in the system, which we assume would make it most useful for identifying and targeting specific areas on the landscape for monitoring, mitigations, and long-term reduction of conflict that would apply beyond collared elephants. Tortuosity-defined staging occurred on a vast majority of agricultural use days, was dispersed throughout the study area, and was the most reliable predictor of agricultural use based on PPV and NPV. We assume that these traits may be most useful for prediction of agricultural incursions from GPS movement data and response by wildlife rangers, which would be limited to collared elephants.

Our mechanistic unsupervised approach helped test assumptions and identify two distinct types of staging, but this limited our ability to assess the cause of false negatives. Indeed, agricultural use days without staging appeared to have different movement patterns (Figure 4) indicating that elephants may not consistently stage prior to crop use, but we could not interpret agricultural staging rates. To refine understanding of staging behaviour, future efforts could employ supervised classification based on the timing and movement patterns identified in this study. These usually appeared distinct and consistent enough to identify visually in the movement track.

The distinction in both movement and environmental correlates for staging defined using tortuosity and behavioural state appeared to be linked to gradients in the juxtaposition between protected and cultivated land. In this system, abrupt transitions between protected areas and unprotected cultivated land were related to higher amounts of tortuosity-based staging events. Protected areas in

TABLE 2 Generalized logistic mixed models for environmental predictors of staging areas using the behavioural state and tortuosity metrics. Coefficient estimates and 95% confidence intervals are reported on the log odds scale: 95% confidence intervals for tortuosity and behavioural state that do not overlap are bolded. Land use type is reported with 'not protected' as the reference level. Drainages is reported with 'not within 250m' as the reference level.

Coefficient	Tortuosity		Encamped Behavioural State	
	Log odds	95% CI	Log odds	95% CI
Intercept	-1.11	[-1.22, -1.01]	-3.36	[-3.52, -3.20]
Percentage of forest (250m)	1.56	[1.39, 1.73]	1.54	[1.37, 1.70]
Percentage of agriculture (1500m)	-2.41	[-2.54, -2.28]	-0.61	[-0.80, -0.41]
Proportion settlements (250m)	-0.34	[-0.38, -0.30]	-0.29	[-0.34, -0.24]
Slope	-0.1	[-0.12, -0.08]	0.14	[0.12, 0.16]
Land use type [limited use]	0.07	[0.03, 0.10]	-0.4	[-0.45, -0.34]
Land use type [protected]	0.32	[0.28, 0.36]	-0.12	[-0.19, -0.05]
Drainages [within 250m]	0.28	[0.25, 0.32]	0.09	[0.03, 0.14]
Autocovariate	0.55	[0.53, 0.57]	0.82	[0.79, 0.85]
Random effects	$s^2_{ID}=0.09$		$s^2_{ID}=0.26$	

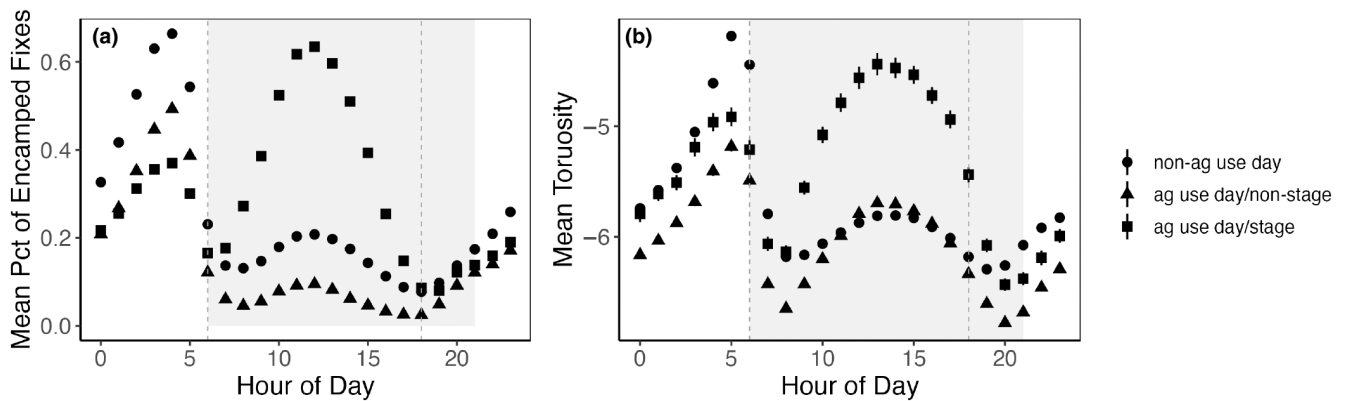


FIGURE 4 Hourly patterns for the encamped behavioural state and tortuosity metrics are shown for agricultural (ag in legend) use days with staging days (squares), non-staging agricultural use days (triangles), and non-agricultural use days (circles). Activity patterns are calculated for each individual and bars represent 95% confidence intervals. (a) shows the mean percentage (Pct) of encamped behaviour fixes for each hour among all elephants. (b) shows the mean tortuosity for each hour among all elephants. Dashed lines indicate approximate sunrise and sunset, and the shaded box represents the time considered for staging events (6 AM–9 PM).

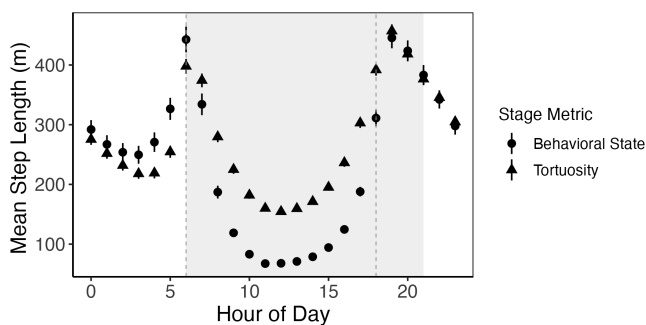


FIGURE 5 Mean hourly step length for days with encamped behavioural state (circles) and tortuosity (triangles) defined staging events, highlighting that events identified using behavioural states show notably lower displacement relative to those identified using tortuosity. The mean step lengths are calculated by individual, and bars correspond to 95% confidence intervals. Dashed lines indicate approximate sunrise and sunset, and the shaded box represents the time considered for staging events (6 AM–9 PM).

TABLE 3 Negative predictive value (NPV) and positive predictive value (PPV) results from ensemble outputs.

Metric	Type	Movement only, %	Agricultural filter, %
Encamped Behavioural State	NPV	64	63
	PPV	56	65
Tortuosity	NPV	87	83
	PPV	51	93

the study system only allow tourism, meaning elephant behaviour in such areas is less inhibited by human interaction. In contrast, behavioural state-defined staging events occurred more often in limited use areas (e.g. community conservancies) and unprotected land, which are prone to regular livestock grazing and human activity during the day. Overall, this embedded strategy appeared to put elephants in closer proximity to agriculture with the trade-off of

reduced movement that may limit access to water and forage during the day (Pomeroy et al., 2008).

The definition of wildlife movement behaviours that can identify pre-crop raiding behaviour provides an opportunity for planned management activities to mitigate conflict (Blackwell et al., 2016). For example, known staging hotspots could be regularly monitored during the crop season when the risk of conflict is highest to warn communities about potential conflict and proactively deploy deterrent mitigations. If identified hotspots are widely used, such spatiotemporal management action can potentially impact non-collared crop-raiders. In addition, spatial attributes of staging could be used towards long-term mitigation planning, such as targeted use of unpalatable buffer crops, fencing, and alternative income programs in farms near staging hotspots (Chang'a et al., 2016). In this system, areas with relatively more behavioural state-defined staging areas would be most suited to these approaches (Figure 3; Appendix S2).

Conflict prediction and proactive approaches to mitigate negative interactions have shown many benefits for wildlife and human communities (Shaffer et al., 2019). At the same time, approaches that produce many false positives are not useful in scenarios with limited management capacity to respond (Fang et al., 2019). The use of tortuosity combined with information on distance to agriculture was able to drastically reduce false positives while keeping false negatives low, which suggests that this approach could be valuable in predicting incursions when paired with real-time GPS data. Our ensemble approach allows comparison across multiple metrics to derive the most suited for a specified task, in this case identifying staging behaviour from real-time GPS data. In future work, predictive ability could possibly be improved by combining metrics, although they would need to perform similarly for the embedded (behavioural state, net displacement) or meandering (tortuosity, persistence velocity, step length) staging types. Machine learning approaches that can be trained using multiple metrics and improved over time (Wang, 2019) may be a promising approach to pursue building off lessons from this analysis.

Understanding the complexity of conflict behaviours in wildlife is crucial to evaluate spatial and temporal heterogeneity in conflict risk and develop effective mitigation strategies. While our study used African elephants to test staging behaviour, the approach is translatable to other species that have been described employing such behaviours (Marchinton, 1995; Mekonnen et al., 2012; Wilson et al., 2015), and other metrics that we tested may prove better in different systems. Further research may be most productive for species in ecosystems with landscape traits that appear to drive staging, areas with buffer zones or corridors that may facilitate staging, or where climate change is expected to shift conflict risk (Bautista et al., 2021; Shaffer et al., 2019). Such investigations can play a pivotal role in motivating mitigation efforts and informing land use planning initiatives that incorporate behavioural complexity into human-wildlife conflict risk.

AUTHOR CONTRIBUTIONS

Nathan R. Hahn and George Wittemyer conceived the study and developed the analytical framework. Nathan R. Hahn performed the analysis. Jake Wall and Kristen Denninger-Snyder provided insights on the analysis framework. Nathan R. Hahn led the writing of the manuscript with contributions from all authors. Jake Wall, Kristen Denninger-Snyder, Wilson Sairowua, Marc Goss, Stephen Ndambuki, Ernest Eblate, Noel Mbise and Sospeter Kiambi led the elephant collaring and acquisition of telemetry and spatial data. All authors have commented and approved the final version of the manuscript.

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CONFLICT OF INTEREST STATEMENT


The authors declare they have no conflict of interests.

DATA AVAILABILITY STATEMENT

Elephant GPS data have not been archived given their highly sensitive nature. Interested readers can contact the corresponding author directly for inquiries. Example code is presented in the [Supporting Information](#).

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SUPPORTING INFORMATION

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

Appendix S1. Descriptions and parameterizations of all movement metrics.

Appendix S2. Interactive Map: Interactive map of relative difference in staging occurrence for behavioral state-defined staging (warmer colors, positive values) and tortuosity defined staging (cooler colors, negative values).

Appendix S3. Example script for staging classification using tortuosity movement metric, including calculation of the metric and combination testing.

Appendix S4. Example script of ensemble staging classification using tortuosity movement metric showing how individual combination results were combined for ensemble classification.

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