DISSERTATION

THE SPATIAL AND BEHAVIORAL ECOLOGY OF HUMAN-ELEPHANT CONFLICT

Submitted by

Nathan Ravi Hahn

Graduate Degree Program in Ecology

In partial fulfillment of the requirements

For the Degree of Doctor of Philosophy

Colorado State University

Fort Collins, Colorado

Fall 2022

Doctoral Committee:

Advisor: George Wittemyer

Eric Dinnerstein
Sarah Reed
Colleen Webb

ABSTRACT

THE SPATIAL AND BEHAVIORAL ECOLOGY OF HUMAN-ELEPHANT CONFLICT

Habitat conversion to farmland has increased human-wildlife interactions that often lead to conflict, injury, or death for people and animals. To conserve wide-ranging species in human-modified landscapes it is essential to understand how animals selectively use or avoid cultivated areas. Use of agriculture leads to human-wildlife conflict, but evidence suggests that substation behavioral and spatial variation occurs in how much individuals may use agricultural lands, how they alter their movement behavior, and the impact this has on overall foraging strategies. Therefore, understanding the behavioral and landscape drivers of human-wildlife conflict is critical for managing wildlife populations. This is particularly relevant for wild elephant populations, as human-elephant conflict account for many of the conflict cases in Africa and Asia. I use a GPS dataset of 86 free-ranging elephants in the Serengeti-Mara ecosystem spanning Kenya and Tanzania to explore the spatial and behavioral ecology of human elephant conflict. I discuss my findings in the context of the possible mechanisms driving inter- and intra-individual variation, the ecological and management implications for this variation, applications to other conflict-prone species, and directions for future research.

In the first chapter, I analyzed GPS data of 66 free-ranging elephants in the Serengeti-Mara ecosystem to quantify their use of agriculture. I then examined factors influencing the level of agricultural use, individual change in use across years, and differences in activity budgets associated with use. Using clustering methods, the data grouped into four agricultural use tactics: rare (<0.6% time in agriculture; 26% of population), sporadic (0.6-3.8%; 34%), seasonal (3.9-12.8%; 31%), and habitual (>12.8%; 9%). Sporadic and seasonal individuals represented two thirds (67%) of recorded GPS fixes in agriculture, compared to 32% from habitual individuals. Increased agricultural use was associated with higher daily distance traveled and larger home range size, but not with age or sex. Individual tactic change was

prevalent and the habitual tactic was maintained in consecutive years by only five elephants. Across tactics, individuals switched from diurnal to nocturnal activity during agricultural use, interpreted as representing similar risk perception of cultivated areas. Conversely, tactic choice appeared to be associated with differences in risk tolerance between individuals. Together, these results suggest that elephants are balancing the costs and benefits of crop usage at both fine (e.g., crop raid events) and long (e.g., yearly tactic change) temporal scales. The high proportion of sporadic and seasonal tactics also highlights the importance of mitigation strategies that address conflict arising from many animals, rather than targeted management of habitual crop raiders. This approach can be applied to other species and systems to characterize individual variation in human resource use and inform mitigations for human-wildlife coexistence.

In the second chapter, I explore how elephants shift space use and movement prior to conflict. Staging behavior 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. I developed an algorithmic approach based on omission-commission testing to assess the efficacy of six widely used metrics of animal movement to identify staging behavior prior to agricultural incursions. I applied this approach to GPS data from 55 African elephants in the Serengeti-Mara ecosystem and found tortuosity and HMM-derived behavioral states to be the most effective for identifying staging events. I 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, I tested the viability of algorithms using movement and spatial metrics to predict crop incursions based on GPS data. This approach identified staging behavior 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 behavioral 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. This work shows some of the challenges and advantages of using animal behavior to assess temporal and spatial heterogeneity in human-wildlife conflict and demonstrates the need to further incorporate animal movement data into conflict management approaches. This approach is extendable to other conflict-prone species to assess pre-conflict behaviors and space use. Fine scale movement data applied to management aims allows targeted and proactive mitigation and can facilitate effective spatial planning.

In the third chapter, I draw on my findings and others showing that elephant space use is highly structured by human activity and that the population is structured by the degree to which individuals' crop-raid. I analyzed GPS data from 56 free-ranging elephants to assess drivers of resource selection strategies and the spatial structure of agricultural selection in relation to regions of high and low agricultural fragmentation to assess how crop use may drive patterns of resource selection and space use within a population. I found wide variation in resource selection coefficient values between individuals, indicating strongly differentiated resource selection strategies across individuals, years, and seasons. Variation was particularly marked during the wet season across years, but individuals were more likely to use a similar strategy in the dry season. Cluster analysis of individual resource selection coefficients indicated they were structured primarily by the degree of crop use in the dry season and time spent in protected and unprotected areas. While crops were avoided at the home range level, controlling for space revealed that crop selection patterns were strongly spatially structured and related to the level of fragmentation. In areas with high fragmentation, large farms and small forest refuges, elephants selected most strongly for areas within 1000m of the protected area boundary. In contrast, elephants selected most strongly for areas 1000-2000m away in areas with low fragmentation, smaller farms, and larger forest refuges. My results highlight how variation in behavioral responses to human development and landscape change structure resource selection and space use, and by extension population distributions. This approach can be applied to other species and systems to characterize individual variation in human resource use and inform mitigations for human-wildlife coexistence.

In the fourth chapter, I explore the collaborative development of technologies to aid in conservation challenges such as human-wildlife conflict. Amid accelerating threats to species and ecosystems, technology advancements to monitor, protect, and conserve biodiversity have taken on increased importance. This has become an increasing area of interest to address human-wildlife conflicts where real-time monitoring and warning systems could play an important role in reducing conflict. While most innovations stem from adaptation of off-the-shelf devices, these tools can fail to meet the specialized needs of conservation and research or lack the support to scale beyond a single site. Despite calls from the conservation community of its importance, a shift to bottom-up innovation driven by conservation professionals remains limited. I surveyed practitioners, academic researchers, and technologists to understand the factors contributing to or inhibiting engagement in the collaborative process of technology development and adoption for field use, as well as identify emerging technology needs. High cost was the main barrier to technology use across occupations, while development of new technologies faced barriers of cost and partner communication. Automated processing of data streams was the largest emerging need, and respondents focused mainly on applications for individual-level monitoring and automated image processing. Cross-discipline collaborations and expanded funding networks that encourage cyclical development and continued technical support are needed to address current limitations and meet the growing need for conservation technologies.

ACKNOWLEDGEMENTS

Words cannot express my gratitude to my advisor, Dr. George Wittemyer, for his invaluable experience and feedback throughout my dissertation. I am equally grateful for my research partners including Dr. Jake Wall, Marc Goss, and Wilson Sairowua from the Mara Elephant Project and Dr. Kristen Denninger-Snyder from the Grumeti Fund. I also could not have undertaken this project without my defense committee, who generously provided knowledge and expertise along the way. Additionally, this endeavor would not have been possible without the generous support from the National Science Foundation, which financed my research.

I am also grateful to those in the Wittemyer lab including Aung, Jenna, Patrick, and Guillaume for their brainstorming sessions over tacos, editing help, and moral support. Special thanks also goes to my classmates and cohort members in the Fish and Wildlife Department that provided so much support along the way. I would also like to recognize the wonderful field assistants and rangers with the Mara Elephant Project and Grumeti Fund who were instrumental to my research.

Lastly, I could not have undertaken this experience without the support of my wife Lauren, my dog Candy, and the rest of my family. Their belief in me has kept me motivated throughout this process. I would also like to thank my dog Candy for all the entertainment she provided on writing breaks.

TABLE OF CONTENTS

CHAPTER 1: RISK PERCEPTION AND TOLERANCE SHAPE VARIATION IN AGRICULTURAL USE FOR A TRANSBOUNDARY ELEPHANT POPULATION

Summary

To conserve wide-ranging species in human-modified landscapes it is essential to understand how animals selectively use or avoid cultivated areas. Use of agriculture leads to human-wildlife conflict, but evidence suggests that individuals may differ in their tendency to be involved in conflict. This is particularly relevant to wild elephant populations. We analyzed GPS data of 66 free-ranging elephants in the Serengeti-Mara ecosystem to quantify their use of agriculture. We then examined factors influencing the level of agricultural use, individual change in use across years, and differences in activity budgets associated with use. Using clustering methods, our data grouped into four agricultural use tactics: rare (<0.6% time in agriculture; 26% of population), sporadic (0.6-3.8%; 34%), seasonal (3.9-12.8%; 31%), and habitual (>12.8%; 9%). Sporadic and seasonal individuals represented two thirds (67%) of recorded GPS fixes in agriculture, compared to 32% from habitual individuals. Increased agricultural use was associated with higher daily distance traveled and larger home range size, but not with age or sex. Individual tactic change was prevalent and the habitual tactic was maintained in consecutive years by only five elephants. Across tactics, individuals switched from diurnal to nocturnal activity during agricultural use, interpreted as representing similar risk perception of cultivated areas. Conversely, tactic choice appeared to be associated with differences in risk tolerance between individuals. Together, our results suggest that elephants are balancing the costs and benefits of crop usage at both fine (e.g., crop raid events) and long (e.g., yearly tactic change) temporal scales. The high proportion of sporadic and seasonal tactics also highlights the importance of mitigation strategies that address conflict arising from many animals, rather than targeted management of habitual crop raiders. Our approach can be applied to other species and systems to characterize individual variation in human resource use and inform mitigations for human-wildlife coexistence.

1. Introduction

The long-term fitness of wide-ranging species in landscapes that have been fragmented by human disturbance depends on resource acquisition and movement trade-offs (Moody et al., 1996; Tucker et al., 2018). Across species, these trade-offs can result in wide variation in how individuals select habitats, use space, and move between heterogeneous landscape patches (Bastille-Rousseau et al., 2019; Hertel et al., 2019; Leclerc et al., 2016). This can result in alternative behavioral tactics, where individuals may express different responses to a given environmental context. In fragmented landscapes, this variation can impact ecological processes such as intraspecies competition, dispersal and reproduction, spread of disease and invasive species, and interactions with humans (Sih et al., 2011). Population-level analyses that average across individuals may miss important differences in the way individuals use habitats, even to the extent where average behavior is not representative of any behavioral tactics (Bastille-Rousseau et al., 2019; Hertel et al., 2019). Yet, it can be difficult to quantify variation and identify trade-offs when there are strong gradients in human activity and differences in response among individuals (Johnson et al., 2015). In the face of rapidly changing landscapes, the link between movement and ecological processes has increased the importance of studying how human activity and land conversion structure animal behavior (Spiegel et al., 2017; Tucker et al., 2018; Wall et al., 2021). Long-term GPS datasets can provide the means to assess the environmental factors that influence behavioral tactics across a population and provide critical context for conservation actions.

In human-dominated landscapes with hunting or persecution, wildlife often perceive humans as a threat and in turn seek to minimize encounters through spatial and temporal avoidance (Gaynor et al., 2019). Despite the risk, animals may also seek out areas of human activity that provide high-quality food resources (Stillfried et al., 2017). This creates trade-offs between foraging and predation risk in human-dominated areas. Behavioral variation emerges as differences in risk tolerance and perception drive decision making around this trade-off, and can in turn lead to impacts on survival as some individuals spend more time in areas with people (Sih et al., 2011). These foraging decisions should be realized in an animal's space use, reflected in both long-term trends in use and avoidance of anthropogenic resources (i.e. risk tolerance) (Stillfried et al., 2017), and short-term movement strategies to avoid people in space and time (i.e. risk perception) (Gaynor et al., 2018). Tolerance and perception of risk are generally linked, so that animals with a higher perception of risk will tolerate it less, thereby driving individual differences in the use of human-dominated areas and leading to alternative tactics in accessing anthropogenic resources (Dingemanse et al., 2010; Ducros et al., 2020).

Human-wildlife conflict due to increased land conversion and human population growth within wildlife ranges is a critical issue, given that wide-ranging large mammals bear most of the cost of this conflict and many are either critically endangered or rapidly declining (Ripple et al., 2015; Woodroffe et al., 2005). Across systems and species, evidence suggests that there is large variation in the propensity of individuals within a population to be involved in conflict with humans (Chiyo and Cochrane, 2005; Hertel et al., 2019; Linnell et al., 2008). This is particularly well-documented in wild elephant populations who raid crops (Mumby and Plotnik, 2018). Yet the behavioral complexity of conflict is poorly understood, and presents challenges for conflict management given that solutions will likely need to address multifaceted aspects accounting for behavior, landscape, and management resources (Blackwell et al., 2016).

For elephants, crop-raiding can provide a nutrient-rich food source but introduces large risks that can impact short-term survival as a result of retaliatory attacks by farmers using spears, arrows, and poison (Hoare, 2015). Diel activity in elephants is known to be strongly influenced by human presence (Gaynor et al., 2018; Ihwagi et al., 2018), and human development is a severe restriction on elephant space use across Africa (Wall et al., 2021). Elephants are known to alter their behavior preceding and following crop raiding (Troup et al., 2020), and use forest refuges during the day to reduce exposure in agricultural areas (Songhurst et al., 2016). Crop raiding has also been consistently reported as sex- and age-biased towards dispersed adult males (Chiyo and Cochrane, 2005; Smit et al., 2019). Males may be more likely to raid crops because they are more socially independent than females and require more energy to enter and maintain their reproductive state (Chiyo et al., 2011). In African savannah elephants (*Loxodanta africana*), the majority of conflict is often attributed to a few 'problem individuals' who habitually raid crops while most of the population may raid occasionally or avoid the risk completely (Chiyo and Cochrane, 2005; Hoare, 2001). This suggests that there are multiple behavioral tactics related to agricultural use. A plethora of mitigation efforts have been centered around deterring habitual crop raiders through hazing, translocations, and removal (Hoare, 2015). However, there is limited understanding on the complexity of crop raiding behavior and the extent to which individuals use agricultural over time, partly due to the difficulty in obtaining detailed longitudinal data on individual crop use behaviors (Mumby and Plotnik, 2018).

Here, we use a long-term GPS tracking dataset to characterize and explore individual variation in crop raiding behavior to address the following objectives. First, we outline and implement an approach to assign tracked individuals in a free-ranging population of elephants into distinct agricultural-use tactics. Next, we assess the relationship between agricultural-use, life-history traits, and general space use. To determine whether tactics are consistent over time, we then quantify intra-individual variation in tactics between years. Finally, to assess differences in risk perception across tactics, we assess the impact of tactic choice on an individual's activity budget between agricultural and non-agricultural movement phases. Because crop raiding is thought to be mainly perpetrated by a small percentage of males, we expected to find agricultural-use tactics of rare, seasonal, and habitual use and increasing agricultural-use strongly correlated with males and older adults. We expected individual switching between tactics would be minimal, but that larger home range sizes would facilitate increased switching. Finally, we expected that activity budgets would be impacted by agricultural use and indicate lower risk perception among seasonal and habitual tactics. We discuss our findings in the context of the possible mechanisms driving variation in elephants' use of agriculture, the implications of diverging tactics for managing human-wildlife conflict, and directions for future research.

2. Methods

Study Area

The study was conducted in the Serengeti-Mara Ecosystem; a 40,000 km^2 savannah ecosystem in southwestern Kenya and northwestern Tanzania (Fig 1). The elephant population in the ecosystem was estimated at 7,535 individuals in 2014 (Mduma et al., 2014). The core area of the system is formed by the Masai Mara National Reserve in Kenya and Serengeti National Park in Tanzania, and is buffered by game reserves and community-managed conservancies with limited livestock grazing. The remaining area is unprotected and made up of private and community land used for agriculture and pastoralism. The seasonal rainfall distribution is strongly bimodal, with a short wet season from November to January and a long wet season from March to June. Vegetation types range from productive short-grass communities to mixed tall-grass, savannah, woodland, and Afromontane forests (Ogutu et al., 2009). Crop agriculture is primarily grain crops and has two growing seasons corresponding to the bimodal rainfall pattern in the system. Crops are mainly grown in unprotected areas, and the overall extent of agricultural land has expanded from 37.0% of the region in 1984 to 54.0% in 2018 (Veldhuis et al., 2019). Human-elephant conflict fluctuates with crop cycles, but incidences have risen overall in conjunction with agricultural expansion (Denninger-Snyder et al., 2019; Mukeka et al., 2019).

Tracking Data

We used GPS relocation data collected from March 2011 to December 2019 for 84 elephants spanning the Mara (n = 51) and western Serengeti (n = 31) regions of the ecosystem (Fig 1). In the Mara, elephants were selected opportunistically for collaring to provide a spatial representation of the area and monitor elephants at risk for poaching and conflict. In the Serengeti, elephants were selected based on dry-season population density. Females selected for collaring each represented a distinct family group, while selected males were socially independent at the time of collaring. Elephants were immobilized and fitted with GPS collars (Savannah Tracking and Animal Wildlife Tracking) following procedures established by the Kenya Wildlife Service and Tanzania Wildlife Research Institute and approved by Colorado State

University's IACUC committee (protocol no. 18-7744A and 19-9431A). Age classes were assigned to all collared elephants as young adults (15– 34) and old adults (>35) based on ageing criteria established from known elephant populations (Moss, 2001). Individuals that did not overlap with at least one crop season or ranged outside of available spatial layers were excluded, resulting in a dataset of 66 elephants, 32 male and 34 female, for the analysis (Table A1). GPS relocations were set to 1 hour or 30-minute sampling, but to evaluate crop use equally among elephants we down-sampled to a standard hourly fix rate. Precision error was negligible in comparison with the scale of the spatial covariates. All 66 animals were used to define agricultural use tactics. A subset of 62 individuals with multi-year datasets were used to quantify and model annual changes between tactics. A subset of 54 individuals with >95% fix success rate were used for behavioral state estimation (McClintock et al., 2013).

Environmental Data

Spatial and environmental covariates were compiled to analyze agricultural use and movement strategies (Table A2). Agricultural coverage was derived from a 30-m Landsat land cover classification of the Serengeti-Mara ecosystem published in Veldhuis et al., 2019. Forest cover, defined as areas with over 30% canopy cover in 2019, was determined from the 30-m Landsat forest cover change product in Google Earth Engine (Hansen et al., 2013). Rivers were manually digitized and classified as either permanent or seasonal using ground truthing and local knowledge (TWCM and FZS, 1996; Tyrrell et al., *in press*). We sampled these data at 30-meter resolution and calculated Euclidean distance to agricultural edge, forest edge, and rivers using R version 4.0.3 (R Core Team, 2013). Slope was calculated based on the 30-meter SRTM digital elevation model (Farr et al., 2007). Human footprint was assessed using the 1000-m Global Human Modification layer for 2015 (Kennedy et al., 2019). From these layers, covariate values were extracted for each GPS fix and standardized to improve model convergence. Because the exact timing of the short and long rain crop cycle varied annually, we used years as the agricultural-use sampling unit. To avoid splitting data within a single crop season, we assigned an adjusted-year variable and chose April 1^{st} as the cutoff point that best reflected when most fields were fallow in the northern and southern regions of the system and conflict is at a low point (unpublished data, Hahn 2020).

Tactic Clustering

For our first objective, we sought to classify and define tactics related to agricultural use in the population. We considered a tactic as a group of elephants displaying similarity in the intensity and temporal patterns of their agricultural use. Due to sampling constraints, some years lacked any high-use individuals. A two-step approach was used to keep tactic definitions consistent between years. First, we aggregated agricultural use for the entire track of each individual i to identify tactics and determine thresholds of agricultural use between tactics. Second, tactic thresholds were used to predict $T_{i,y}$, the tactic used by individual i in year y, based on yearly agricultural use. To characterize tactics, we defined two crop use measurements that reflected the intensity and temporal fluctuations in use: mean use μ_i (the number of relocations in agriculture versus the total relocations for an individual) and the 90-day maximum agricultural use m_i (maximum value of a 90-day moving average of agricultural use for an individual-year, averaged over years). A moving average was chosen to smooth fluctuations at smaller time scales and clarify yearly peaks in usage. A 90-day window was selected to represent a typical grain crop growing season (unpublished data). To identify tactic clusters among individuals in the population, we implemented Gaussian Mixture Models (GMMs) using the MClust package for R (Bastille-Rousseau et al., 2019; Scrucca et al., 2016). We fit three candidate models using mean use, maximum use, and both mean and maximum use. We used Bayesian Information Criterion to select the optimal number of clusters for each of the three models (Scrucca et al., 2016), including one cluster as a possibility. We used predictive performance to select the top model, evaluated using repeated 10-fold cross-validation with 20 repeats. Additional information on agricultural use measurements and model fitting can be found in Appendix A.2 Agricultural Tactics Clustering.

To address our second objective to identify correlates of agricultural use, we conducted generalized linear mixed models with a gaussian link and used individual-year mean agricultural use as the response variable. Candidate models were evaluated using corrected Akaike Information Criterion (AICc) to adjust for the small sample size of the dataset. Covariates were chosen based on our expectation that age, sex, and movement would influence use: age class, sex, individual-year home range size, and individual-year mean daily displacement. We included a random effect for individual ID. Home range size was determined using 95% minimum convex polygons in the adeHabitatHR package for R (Calenge, 2015a).

Tactic change

For our third objective to quantify individual tactic change between years, we assessed change using individual-year tactics $T_{i,y}$. Each individual year was coded as a change or non-change year, where tactic change was defined as $T_{i,y-1} \neq T_{i,y}$. We discounted the first year for each individual because a previous tactic could not be determined. To investigate drivers of tactic change, we conducted generalized linear mixed models with individual-year tactic change as the response variable. Tactic change, coded as change or non-change, was modeled with a binomial distribution. We included a random effect for individual ID. Candidate models were evaluated using corrected Akaike Information Criterion. Covariates were chosen based on expectations that age, sex, and prior tactic would influence tactic change: age class, sex, individual-year home range size, prior year tactic, and an interaction between age class and sex.

Behavioral State Comparisons

For our fourth objective to assess differences in activity budgets when using agriculture or not, we used hidden Markov models (HMMs) (Morales et al., 2004) to infer latent behavioral states from the movement path. HMMs allow estimation of behavioral states based on the speed and turning angle between each pair of GPS relocations (Langrock et al., 2012), but require that the number of behavioral states be chosen before fitting the models. We considered HMMs with three behavioral states, based on prior findings from Polansky et al. (2015): S1 – 'encamped' characterized by slow speeds and high tortuosity associated with localized foraging and resting, S2 – 'meandering' characterized by moderate speeds and meandering directions associated with active foraging, and S3 – 'directed walk' characterized by high speeds and directional travel associated with dispersal behaviors (Fig S3). To improve our behavioral state estimates and investigate the effect of environmental variables on behavioral decisions, we included covariates for the state transition probabilities. HMMs estimate a state transition probability matrix (i.e. the probability of transitioning from encamped to foraging), and we applied covariates to this matrix using mixed linear regression models with a gaussian link (Patterson et al., 2009). Covariates were selected based on expectations that terrain and distance to human and natural features would affect movement behavior: distance to the nearest agriculture edge (allowing negative values for fixes within agriculture), distance to forest, distance to permanent and seasonal water, slope, human footprint, and a random effect for individual identity (Table A2). We constructed 10 candidate models and used Akaike Information Criteria to select the best covariate formulation. HMMs were evaluated graphically using pseudo-residuals and by comparing observed step length and turning angle distributions with simulated data generated from the model (Vogel et al., 2020). Following model selection, the Viterbi algorithm was used to estimate a behavioral state for each GPS relocation, which in turn were used to calculate activity patterns. Model fitting and evaluation was implemented using the momentuHMM package for R (McClintock and Michelot, 2018). Additional information on model fitting and diagnostics can be found in Appendix A.3 Hidden Markov Models.

To infer risk perceptions we contrasted 24-hour activity patterns between periods in and outside of agriculture, given that shifts in activity (i.e., diurnal to nocturnal) to avoid human activity are a good indicator of risk perception (Gaynor et al., 2018). To compare movement in and out of agriculture, we defined an agricultural use movement phase (e.g., Nathan et al., 2008) (Fig A9 & A10). Phases were defined as any GPS relocations within 6 hours (before or after) of a relocation in agriculture, based on findings from Troup et al. 2020 on elephant movement before and after crop raiding. To consider changes in activity between phases, we constructed kernel density estimates of state-level 24-hour activity to quantify 1) the intra-tactic change in activity between agricultural use and non-use phases; and 2) inter-tactic differences in activity. Change in activity was quantified using the estimated overlap (OV) between activity density estimates (Ridout and Linkie, 2009). For intra-tactic change, we estimated overlap OV_{intra} of activity density estimates in agricultural use and non-use phases by individual-year. A generalized linear mixed model was used to assess OV_{intra} in relation to tactic and state, treating the individual as a random effect. OV_{intra} was modeled with a gaussian distribution. For inter-tactic differences, we estimated overlap OV_{inter} of activity density estimates for each unique tactic pair (n = 6 per state). A generalized linear model with gaussian link was used to assess OV_{inter} in relation to agricultural use phase, state, and tactic pair.

3. Results

The 66 elephants used for the analysis produced 939,844 GPS relocations, resulting in a median of 12,587 fixes (Masai Mara = 15,166, Serengeti = 11,016) per elephant. The elephants spent 31.7% of time in core areas, 47.5% in buffer areas, and 20.9% of time in areas with no formal protections, while 4.83% of time was spent in agriculture. The median distance from home range center to the nearest agriculture area was 2.97 km (sd = 4.7km).

Tactic Clustering

For our first objective, we identified four agricultural use tactics. From the Gaussian Mixture Models, we found that mean agricultural use (cv error = 1.36%) best describes clusters among individuals, and identified four clusters according to BIC rankings (Fig S2). The maximum agricultural use model was slightly less accurate (cv error = 1.91%) and produced just two clusters, while the model with mean and maximum use performed markedly worse (cv error = 15%) and identified four clusters (Hahn et al., 2021). Using the clusters produced in the top model of mean agricultural use, we defined the four tactics as: T1 – rare (<0.6% mean agricultural use) with consistently low rates of agricultural use; T2 – sporadic (0.6-3.8% mean use) characterized by low to moderate seasonal agricultural use; T3 – seasonal (3.9-

12.8% mean use) characterized by intensive seasonal agricultural use; and T4 – habitual (>12.8% mean use) characterized by consistent high rates of use throughout the year (Fig 2). Using these cluster definitions, 202 individual-years from 66 individuals were classified into tactics. Of the 66 elephants, 53 (80%) spent at least one year in the sporadic, seasonal, or habitual classes, while 13 (20%) were found to only use the rare class. Overall, rare use was observed in 26% of the individual-years, while sporadic made up 34%, seasonal was 31%, and habitual was 9%. Sporadic and seasonal individuals represented two thirds (67%) of recorded GPS fixes in agriculture, compared to 32% from habitual individuals and 1% from rare individuals. Females made up 72% of rare, 44% of sporadic, 48% of seasonal, and 33% of habitual tactic classes (Fig 3a). In our second objective, the model with mean daily displacement and home range size performed best according to AICc (Table A3). We found that mean daily displacement was positively correlated with agricultural use ($\beta = 0.05$, 95% CI [0.01, 0.08]), while home range had a marginal effect ($\beta = 0.01$, 95% CI [-0.001 – 0.01]) (Table 1). Among-individual variation of the intercept was 0.003. A competing model that included sex was found (ΔAICc = 0.95), but sex had a negligible effect on agricultural use (Table A3).

Tactic Change

For our third objective, 136 individual-years (mean of 3.06 years per individual, sd = 1.82) were used to assess tactic change rates after discounting the initial year, for which a change in tactic could not be determined. Individual-years in the rare use tactic (n = 32) had the lowest rate of tactic change from the prior year (rate = 0.12, 95% CI = [0.07, 0.18], while sporadic (n = 51; rate = 0.35, 95% CI = [0.29, 0.42]), seasonal (n = 43; rate = 0.37, 95% CI = [0.30, 0.45]), and habitual (n = 10; rate = 0.40, 95% CI = [0.24, 0.56]) all had significantly higher change rates. By sex, tactic change rates were more predictable for females (rate = 0.26, 95% CI = [0.07, 0.30] than males (rate = 0.37, 95% CI = [0.31, 0.42]. The logistic mixed model with age class, sex, and home range size was selected based on AICc (Table A4). The probability of switching tactics increased with home range size ($\beta = 3.24$, 95% CI [0.07 – 7.47]). We also found a significant interaction between age class and sex, where the probability of switching tactics increased for old males and young females (Table 2, Fig 3b). Among-individual variance of the intercept was 1.17 on the log-odds scale. We found a competing model (ΔAICc = 1.1) with only age class and sex.

Behavioral State Comparisons

For our fourth objective, Hidden Markov models were fit to 939,844 GPS relocations, comprising 54 individuals. The Hidden Markov model with a generalized linear mixed model of distance to forest, distance to permanent and secondary rivers, slope, human modification, and distance to agriculture with a polynomial of degree 2 produced the lowest AIC value (Table A5), and diagnostics indicated good model fit (Fig A4, A5).

Using the agricultural use phases (includes movement 6 hours before and after crop usage) and individual-year tactic classifications, habitual individuals spent 70.5% of their time in agricultural use phases, while seasonal spent 38.8%, sporadic 20.53%, and rare 3.59%. Comparing intra-tactic activity density estimates (OV_{intra}) between phases, tactic had a weak effect on activity overlap, indicating similar shifts in activity between tactics (Table 3a, Fig 4). By state, meandering had much higher overlap between phases than encamped (β = 0.17, 95% CI [0.14, 0.20]), as did directed walk (β = 0.14, 95% CI [0.10, 0.17]), indicating that encamped behavior was most affected by agricultural use. Among-individual variance of the intercept was 0.008. In agricultural use phases, individuals showed multiple peaks in encamped behavior while employing a single encamped period out of phase (Fig 4). Relatedly, peaks in exploratory movement also shifted to night when in agricultural use phases, occurring during times considered to be active crop-raiding hours (Troup et al., 2020). Comparison of inter-tactic activity density estimates (OV_{inter}) revealed rare and habitual had the least overlap in activity, sporadic and seasonal had the greatest overlap (β = 0.05, 95% CI [0.00, 0.09]), and overlap differences for remaining pairwise comparisons were marginal (Table 3b). By state, meandering had significantly higher overlap in relation to encamped (β = 0.07, 95% CI [0.04, 0.11]), indicating time budgets for this activity were conserved irrespective of agricultural use tactic (Table 3b).

4. Discussion

The development of effective strategies to mitigate wildlife impacts on humans (or vice versa) is facilitated by understanding the factors that underpin space use in human-dominated landscapes (Sih et al., 2011; Wittemyer et al., 2019). Given the escalation of human-wildlife conflict, characterizing wildlife use of agricultural areas is of particular interest. Our analytical framework to systematically cluster and assess individuals based on use of a human resource helped to define alternative tactics related to agricultural use and disentangle drivers related to the individual and the environment. We classified four distinct tactics in relation to the intensity of agricultural use and found that more individuals are at risk for conflict than previously thought. Given that all individuals studied were in the same ecosystem and could access cultivated areas equally, we interpreted tactic choice as a representation of individual differences in risk tolerance (Stillfried et al., 2017), and shifts in 24-hour activity (day-night ratios) as a representation of risk perception (Gaynor et al., 2018). The similar shift to nocturnal activity for all tactics during agricultural use suggests that perceptions of risk are similar across individuals, while differences in risk tolerance appeared to drive the variation in tactic choice and tactic change. We discuss these findings in relation to the most plausible mechanisms driving variable agricultural use, the implication of diverging tactics on management of human-wildlife conflict, and application to other species.

Tactics differed markedly in occurrence and indicated a large percentage of elephants were at risk of conflict; 66% of individual-years were in the seasonal and sporadic class, while only 9% of individual-years were of the habitual. In contrast to previous research in which bulls were reported to be the dominant perpetrators in elephant crop raiding (Chiyo et al., 2011; Hoare, 2015; Smit et al., 2019), we found that sex was not predictive of mean yearly agricultural use. While our study inherently quantified use by individual elephants, research is still needed on how the tactic choices of individual females may impact the rest of their family group. The prevalence of agricultural usage by females and mixed cow-bull groups across the transboundary ecosystem may be a response to patterns of agricultural expansion along protected area boundaries observed over the last 35 years (Tiller et al., 2021; Veldhuis et al., 2019). Given the restrictions that expanding human development has placed on elephant ranges in Africa (Wall et al., 2021), further research is warranted on the complexities of crop use behavior and the impact of agricultural edge effects on family groups across systems and continents.

We found high rates of individual tactic change across years, indicating the population segment using agriculture is more dynamic than previously thought. Switching was strongest among habitual individuals, to the extent that only five out of 62 animals maintained a habitual use strategy for consecutive years. Further, the increased probability of tactic change for mature adult males supports previous work linking crop raiding to male reproductive strategies (Chiyo et al., 2011), although we lacked observations of male reproductive state in the study population to investigate further. As movement is energetically expensive, the correlation of larger home ranges and higher mean daily displacement with agricultural use suggests that crop usage may be associated with higher energetic expenditure to reach crops. Farmland provides a patch with relatively low search time and high concentration of forage (Branco et al., 2019), which potentially offsets increased energy expenditure. However, the high rates of tactic change between years for habitual and seasonal individuals suggest that maintaining high levels of agricultural use over time may be difficult.

In our assessment of risk perception among individuals, we found that irrespective of tactic, elephants shifted activity during phases of agricultural use to concentrate encamped behavior during the day and shift to predominantly nocturnal directed walk movements. This was consistent with behavior described in other elephant populations while traversing agricultural areas (Songhurst et al., 2016; Tiller et al., 2021), and could be the result of individuals experiencing similar hazing and retaliation from humans. Here, we observed a decoupling of risk perception and tolerance, resulting in a similar spatially explicit movement strategy for all individuals that reduced risk when using human resources and a large variation in the amount of time (interpreted as reflective of variation in tolerance) individuals were willing to spend in human-dominated areas. Our results demonstrate how individuals are balancing the costs of increased risk and energetic expenditure and the benefits of high-quality forage at fine (e.g., agricultural use phases) and long (e.g., yearly tactic change) temporal scales.

We note that our analysis was conducted at a coarse scale where tactics emerged from the underlying differences in movement choices between individuals, and risk was inferred from movement. Resource selection functions can help further investigation of the relationship between tactic choice, space use, and the composition of the agricultural matrix. Further, this analysis used an agriculture classification that did not distinguish between planted and fallow fields. High fidelity annual classification that can identify actively planted fields would aid the detection of crop raiding versus dispersal movements through the agricultural matrix, help to refine tactic definitions, and allow assessment of tactic change at a seasonal scale.

This study highlights the complexity of elephant use of agriculture and the importance of individual variation in management planning. While only five individuals maintained habitual crop raiding levels over multiple seasons, most individuals used agriculture at least sporadically. This implies that a larger percentage of the population is at risk of conflict and may explain why efforts that focus on mitigation or removal of habitual individuals often prove unsuccessful. When many individuals raid occasionally, mitigations that are cheap and easily scalable within local communities should be more effective, such as chili and beehive fencing or unpalatable crops that buffer at-risk farms from elephants (Hoare, 2015). Further, hazing mitigations could be targeted to leverage knowledge on patterns of risk perception. For example, while most hazing applications occur during a raid, applications during times and in locations that elephants perceive to be safe before crop use (e.g., in rest areas during the day) could reduce the overall time spent in agricultural use phases. Because risk perception and movement behaviors are similar among tactics, this hazing strategy would be applicable across a population.

Understanding the individual complexity of conflict behaviors in wildlife is crucial to develop effective mitigation strategies. While our study focused on elephant crop use, the clustering approach is translatable to other species where time spent in specific areas leads to conflict. This may be most productive for species where variation in conflict risk between individuals has already been documented, such as carnivore depredation of livestock and bears accessing human food resources. Such investigations can play a pivotal role in motivating mitigation efforts and land use planning initiatives that incorporate behavioral complexity in human-wildlife conflict hotspots.

5. Tables & Figures

Table 1. Drivers of mean agricultural use for 202 elephant individual-years in the Serengeti-Mara Ecosystem, analyzed using a mixed effects regression. Home ranges were calculated as minimum convex polygons. Fixed effect coefficients are shown with 95% confidence intervals, and highlighted in bold where confidence intervals did not overlap zero. Positive values indicate a covariate was predictive of increased agricultural use. See Table A3 for model selection results.

Term	Estimate	S.E.	95% CI
Intercept	**-0.43**	**0.16**	**-0.73 – -0.12**
Home range	0.01	0.004	0.00 – 0.02
Mean Daily Displacement	**0.05**	**0.02**	**0.01 – 0.08**

Table 2. Drivers of tactic change by individuals between years. Tactic change was assessed using a mixed effects regression with logit link. Fixed effect coefficients are shown with 95% confidence intervals, and highlighted in bold where confidence intervals did not overlap zero. Positive values indicate a covariate was predictive of switching tactics from the previous year. See Table A4 for model selection results.

Term	Estimate	S.E.	95% CI
(Intercept)	-1.61	0.52	-2.98 - -0.72
Sex:Male	-1.71	1.17	-4.64 – 0.33
Age:Old Adult	-0.38	1.14	-3.14 – 1.77
Home Range	3.24	1.76	0.07 – 7.47
Male*Old Adult	2.92	1.71	0.01 – 7.29

Table 3. Factors driving intra- and inter-tactic similarity in circadian activity patterns of elephants. Similarity was quantified using estimated overlap of activity pattern densities. A) Factors affecting intra-individual similarity in activity patterns when in versus outside of agricultural use phases, assessed using a generalized linear mixed model. The intercept includes factor levels for the low use tactic and encamped state. B) Similarity in circadian activity patterns between the four agricultural use tactic classes using a generalized linear model. The intercept contains factor levels for out-of-phase movement, encamped state, and rare-habitual comparison. For both tables, fixed effect coefficients are shown with 95% confidence intervals, and highlighted in bold where confidence intervals did not overlap zero. Positive values indicate greater similarity in comparison to the reference level contained in the intercept.

A. Term	Estimate	S.E.	95% CI
Intercept	**0.65**	**0.03**	**0.58 – 0.72**
Tactic:Sporadic	-0.02	0.03	-0.09 – 0.04
Tactic:Seasonal	-0.01	0.04	-0.08 – 0.06
Tactic:Habitual	-0.02	0.05	-0.10 – 0.06
State:Meandering	**0.17**	**0.02**	**0.14 – 0.20**
State:Directed Walk	**0.14**	**0.02**	**0.10 – 0.17**

B. Term	Estimate	S.E.	95% CI
Intercept	0.84	0.02	0.80 - 0.89
Ag Use Phase:In-phase	-0.004	0.01	-0.03 - 0.02
State:Meandering	**0.07**	**0.02**	**0.04 - 0.11**
State:Directed Walk	0.03	0.02	-0.01 - 0.06
Comp:Rare-Sporadic	0.002	0.03	-0.05 - 0.05
Comp:Rare-Seasonal	0.02	0.03	-0.03 - 0.07
Comp:Sporadic-Seasonal	0.05	0.03	-0.001 - 0.10
Comp:Sporadic-Habitual	0.03	0.03	-0.02 - 0.08
Comp:Seasonal-Habitual	0.04	0.03	-0.01 - 0.09

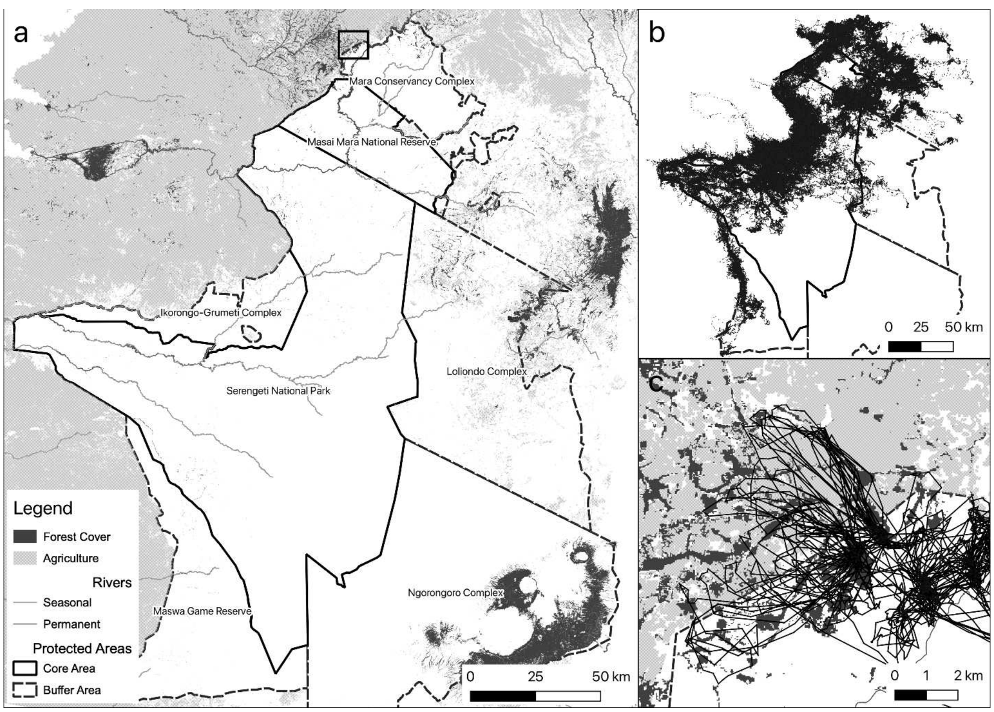

Figure 1. A) The Greater Serengeti-Mara Ecosystem showing core and buffer protected areas, agriculture, forest, and permanent and seasonal rivers. Buffer area boundaries have been simplified. B) Shows the GPS relocations of the 66 individuals included in the study. C) Shows a close up (bounding box in A) of the individual Ivy's GPS track as she makes repeated forays into the surrounding agricultural area.

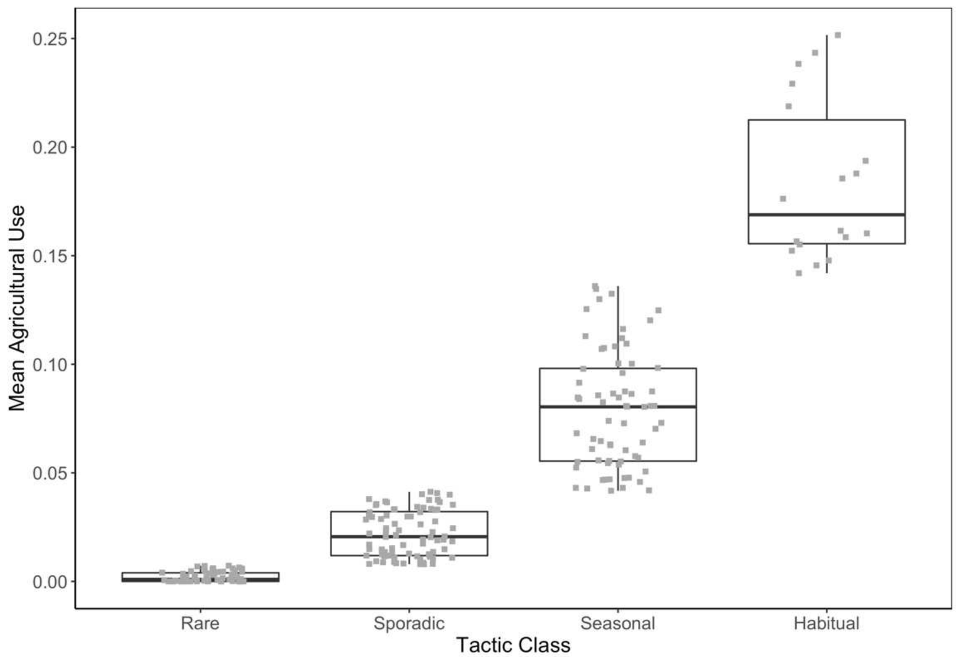

Figure 2. Tactic clusters defined by a univariate Gaussian Mixture Model using mean agricultural use. Boxplots show the distribution of mean agricultural use for each tactic class. Grey squares show the mean agricultural use for each individual used in the classification organized by tactic class.

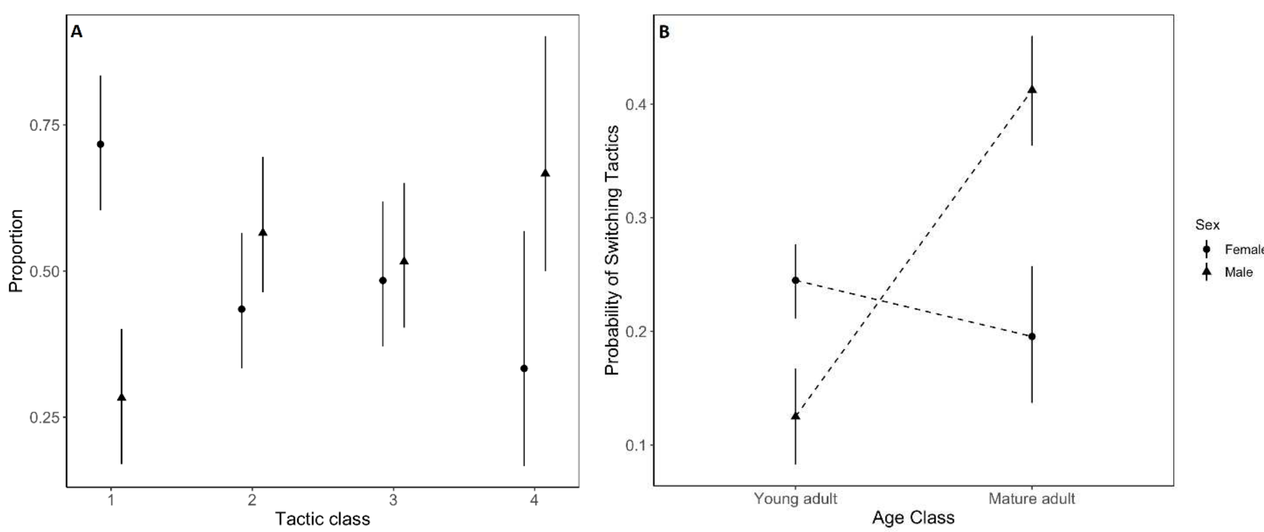

Figure 3. A) Sex proportions for each tactic using individual-year classifications. B) Interaction of age class and sex affecting the probability of switching tactics between years. For both graphs, vertical bars represent 95% confidence intervals.

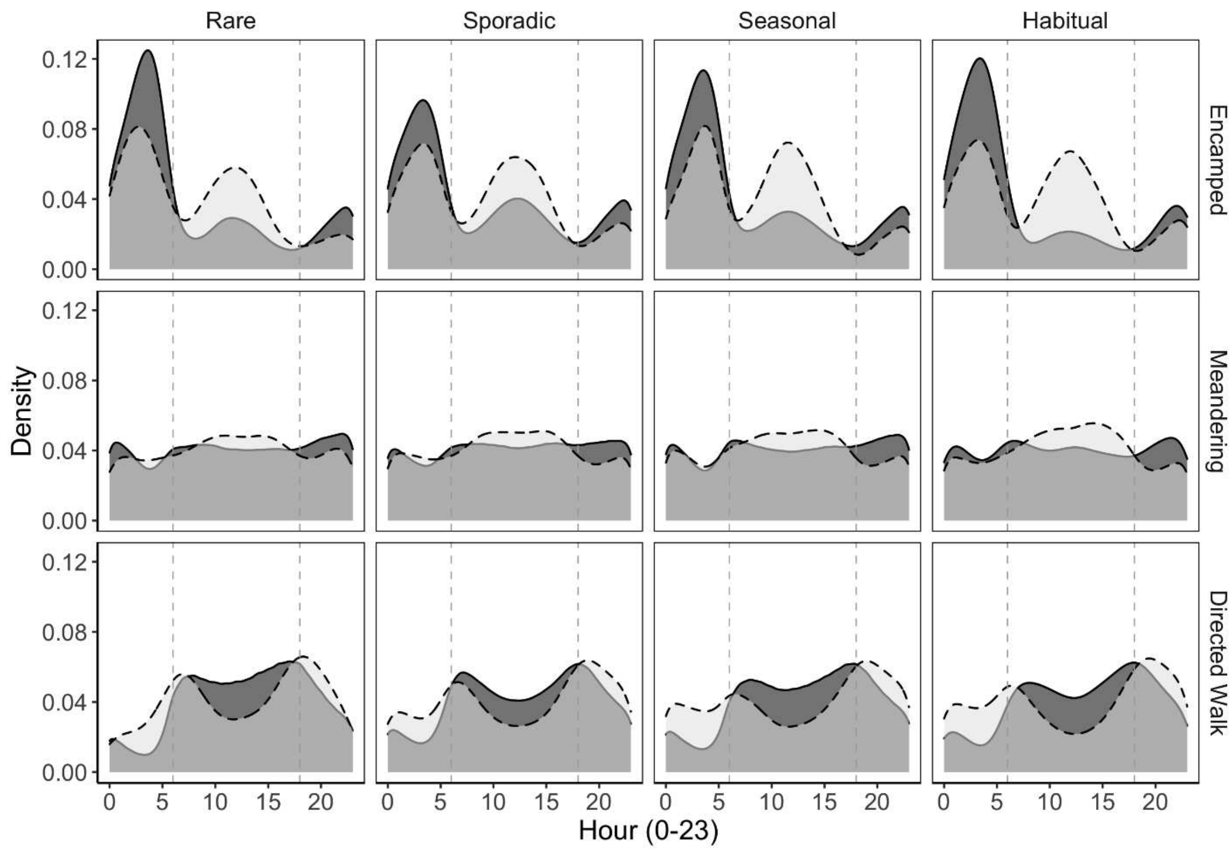

Figure 4. Kernel density estimates for 24-hour activity patterns are shown for agricultural (dashed line, grey fill) and non-agricultural (solid line, dark grey fill) use phases. Density estimates are stratified by tactic (column) and behavioral state (row). Vertical dashed lines indicate approximate sunrise (6:30am) and sunset (6:30pm) times.

6. References

Bastille-Rousseau, G., Wittemyer, G., Bastille-Rousseau, G., Wittemyer, G., 2019. Leveraging multidimensional heterogeneity in resource selection to define movement tactics of animals. Ecol. Lett. 22, 1417–1427. https://doi.org/10.1111/ele.13327

Blackwell, B.F., DeVault, T.L., Fernández-Juricic, E., Gese, E.M., Gilbert-Norton, L., Breck, S.W., 2016. No single solution: application of behavioural principles in mitigating human–wildlife conflict. Anim. Behav. 120, 245–254. https://doi.org/10.1016/j.anbehav.2016.07.013

Calenge, C., 2015. Home Range Estimation in R : the adehabitatHR Package. R vignette 1–60. https://doi.org/10.1111/j.1365-2656.2006.01186.x

Chiyo, P.I., Cochrane, E.P., 2005. Population structure and behaviour of crop-raiding elephants in Kibale National Park, Uganda. Afr. J. Ecol. 43, 233–241. https://doi.org/10.1111/j.1365-2028.2005.00577.x

Chiyo, P.I., Lee, P.C., Moss, C.J., Archie, E.A., Hollister-Smith, J.A., Alberts, S.C., 2011. No risk, no gain: Effects of crop raiding and genetic diversity on body size in male elephants. Behav. Ecol. 22, 552–558. https://doi.org/10.1093/beheco/arr016

Denninger-Snyder, K., Mneney, P., Benjamin, B., Mkilindi, P., Mbise, N., 2019. Seasonal and spatial vulnerability to agricultural damage by elephants in the western Serengeti, Tanzania. Oryx 1–11. https://doi.org/10.1017/S0030605318001382

Dingemanse, N.J., Kazem, A.J.N., Réale, D., Wright, J., 2010. Behavioural reaction norms: animal personality meets individual plasticity. Trends Ecol. Evol. 25, 81–89. https://doi.org/10.1016/j.tree.2009.07.013

Ducros, D., Morellet, N., Patin, R., Atmeh, K., Debeffe, L., Cargnelutti, B., Chaval, Y., Lourtet, B., Coulon, A., Hewison, A.J.M., 2020. Beyond dispersal versus philopatry? Alternative behavioural tactics of juvenile roe deer in a heterogeneous landscape. Oikos 129, 81–92. https://doi.org/10.1111/oik.06793

Farr, T.G., Rosen, P.A., Caro, E., Crippen, R., Duren, R., Hensley, S., Kobrick, M., Paller, M., Rodriguez, E., Roth, L., Seal, D., Shaffer, S., Shimada, J., Umland, J., Werner, M., Oskin, M., Burbank, D., Alsdorf, D.E., 2007. The shuttle radar topography mission. Rev. Geophys. https://doi.org/10.1029/2005RG000183

Gaynor, K.M., Branco, P.S., Long, R.A., Gonçalves, D.D., Granli, P.K., Poole, J.H., 2018. Effects of human settlement and roads on diel activity patterns of elephants (Loxodonta africana). Afr. J. Ecol. 56, 872–881. https://doi.org/10.1111/aje.12552

Gaynor, K.M., Brown, J.S., Middleton, A.D., Power, M.E., Brashares, J.S., 2019. Landscapes of Fear: Spatial Patterns of Risk Perception and Response. Trends Ecol. Evol. 34, 355–368. https://doi.org/10.1016/j.tree.2019.01.004

Hahn, N., Wall, J., Denninger-Snyder, K., Goss, M., Sairowua, W., Mbise, N., Estes, A.B., Ndambuki, S., Mjingo, E.E., Douglas-Hamilton, I., Wittemyer, G., 2021. Data from: Risk perception and tolerance shape variation in agricultural use for a transboundary elephant population. Dryad Digit. Repos. https://doi.org/https://doi.org/10.5061/dryad.rn8pk0pbn

Hansen, M.C., Potapov, P. V., Moore, R., Hancher, M., Turubanova, S.A., Tyukavina, A., Thau, D., Stehman, S. V., Goetz, S.J., Loveland, T.R., Kommareddy, A., Egorov, A., Chini, L., Justice, C.O., Townshend, J.R.G., 2013. High-resolution global maps of 21st-century forest cover change. Science (80-.). https://doi.org/10.1126/science.1244693

Hertel, A.G., Leclerc, M., Warren, D., Pelletier, F., Zedrosser, A., Mueller, T., 2019. Don't poke the bear: using tracking data to quantify behavioural syndromes in elusive wildlife. Anim. Behav. 147, 91–104. https://doi.org/10.1016/J.ANBEHAV.2018.11.008

Hoare, R., 2015. Lessons From 20 Years of Human–Elephant Conflict Mitigation in Africa. Hum. Dimens. Wildl. 20, 289–295. https://doi.org/10.1080/10871209.2015.1005855

Hoare, R.E., 2001. Management Implications Of New Research On Problem Elephants. Pachyderm 44–48.

Ihwagi, F.W., Thouless, C., Wang, T., Skidmore, A.K., Omondi, P., Douglas-Hamilton, I., 2018. Night-day speed ratio of elephants as indicator of poaching levels. Ecol. Indic. 84, 38–44. https://doi.org/10.1016/j.ecolind.2017.08.039

Johnson, H.E., Breck, S.W., Baruch-Mordo, S., Lewis, D.L., Lackey, C.W., Wilson, K.R., Broderick, J., Mao, J.S., Beckmann, J.P., 2015. Shifting perceptions of risk and reward: Dynamic selection for human development by black bears in the western United States. Biol. Conserv. 187, 164–172. https://doi.org/10.1016/j.biocon.2015.04.014

Kennedy, C.M., Oakleaf, J.R., Theobald, D.D.M., Baruch-Mordo, S., Kiesecker, J.J., 2019. Managing the middle: A shift in conservation priorities based on the global human modification gradient. Glob. Chang. Biol. https://doi.org/10.1111/gcb.14549

Langrock, R., King, R., Matthiopoulos, J., Thomas, L., Fortin, D., Morales, J.M., 2012. Flexible and practical modeling of animal telemetry data : hidden Markov models and extensions 93, 2336–2342. https://doi.org/10.1890/11-2241.1

Leclerc, M., Vander Wal, E., Zedrosser, A., Swenson, J.E., Kindberg, J., Pelletier, F., 2016. Quantifying consistent individual differences in habitat selection. Oecologia 180, 697–705. https://doi.org/10.1007/s00442-015-3500-6

Linnell, J.D.C., Odden, J., Smith, M.E., Aanes, R., Swenson, J.E., Ronn, A., Swen, J.E., 2008. Carnivores and Predation Large carnivores that kill livestock : do " problem individuals " really exist ? Society 27, 698–705.
McClintock, B.T., Michelot, T., 2018. momentuHMM : R package for analysis of telemetry data using generalized multivariate hidden Markov models of animal movement 1–69. https://doi.org/10.1111/2041-210X.12995
McClintock, B.T., Russell, D.J.F., Matthiopoulos, J., King, R., 2013. Combining individual animal movement and ancillary biotelemetry data to investigate population-level activity budgets. Ecology 94, 838–849. https://doi.org/10.1890/12-0954.1
Mduma, H., Musyoki, C., Maliti, K.D., Nindi, S., Hamza, K., Ndetei, R., Machoke, M., Kimutai, D., Muteti, D., Maloba, M., Bakari, S., Kohi, E., 2014. Aerial Total Count of Elephants and Buffaloes in the Serengeti-Mara Ecosystem.
Monitoring, T.W.C., Society, F.Z., 1996. Rivers and small drainages from Greater Serengeti-Mara Ecosystem. Arusha.
Moody, A.L., Houston, A.I., Mcnamara, J.M., 1996. Ideal free distributions under predation risk. Behav. Ecol. Sociobiol. 131–143.
Morales, J.M., Haydon, D.T., Frair, J., Holsinger, K.E., Fryxell, J.M., 2004. Extracting more out of relocation data: building movements models as mixtures of random walks. Ecology 85, 2436–2445. https://doi.org/doi:10.1890/03-0269
Moss, C.J., 2001. The demography of an African elephant (Loxodonta africana) population in Amboseli, Kenya. J. Zool. https://doi.org/10.1017/S0952836901001212
Mukeka, J.M., Ogutu, J.O., Kanga, E., Røskaft, E., 2019. Human-wildlife conflicts and their correlates in Narok County, Kenya. Glob. Ecol. Conserv. 18, e00620. https://doi.org/10.1016/j.gecco.2019.e00620
Mumby, H.S., Plotnik, J.M., 2018. Taking the Elephants' Perspective: Remembering Elephant Behavior, Cognition and Ecology in Human-Elephant Conflict Mitigation. Front. Ecol. Evol. 6, 122. https://doi.org/10.3389/fevo.2018.00122
Nathan, R., Getz, W.M., Revilla, E., Holyoak, M., Kadmon, R., Saltz, D., Smouse, P.E., 2008. A movement ecology paradigm for unifying organismal movement research. Proc. Natl. Acad. Sci. 105, 19052–19059. https://doi.org/10.1073/PNAS.0800375105
Ogutu, J.O., Piepho, H.P., Dublin, H.T., Bhola, N., Reid, R.S., 2009. Dynamics of Mara-Serengeti ungulates in relation to land use changes. J. Zool. 278, 1–14. https://doi.org/10.1111/j.1469-7998.2008.00536.x
Patterson, T.A., Basson, M., Bravington, M. V., Gunn, J.S., 2009. Classifying movement behaviour in relation to environmental conditions using hidden Markov models. J. Anim. Ecol. 78, 1113–1123. https://doi.org/10.1111/j.1365-2656.2009.01583.x
R Development Core Team, R., 2011. R: A Language and Environment for Statistical Computing, R Foundation for Statistical Computing. https://doi.org/10.1007/978-3-540-74686-7
Ridout, M.S., Linkie, M., 2009. Estimating overlap of daily activity patterns from camera trap data. J. Agric. Biol. Environ. Stat. 14, 322–337. https://doi.org/10.1198/jabes.2009.08038
Ripple, W.J., Newsome, T.M., Wolf, C., Dirzo, R., Everatt, K.T., Galetti, M., Hayward, M.W., Kerley, G.I.H.H., Levi, T., Lindsey, P.A., Macdonald, D.W., Malhi, Y., Painter, L.E., Sandom, C.J., Terborgh, J., Van Valkenburgh, B., 2015. Collapse of the world's largest herbivores. Sci. Adv. 1, e1400103–e1400103. https://doi.org/10.1126/sciadv.1400103
Scrucca, L., Fop, M., Murphy, T.B., Raftery, A.E., 2016. Mclust 5: Clustering, classification and density estimation using Gaussian finite mixture models. R J. https://doi.org/10.32614/rj-2016-021
Sih, A., Ferrari, M.C.O., Harris, D.J., 2011. Evolution and behavioural responses to human-induced rapid environmental change. Evol. Appl. 4, 367–387. https://doi.org/10.1111/j.1752-4571.2010.00166.x

Smit, J., Pozo, R.A., Cusack, J.J., Nowak, K., Jones, T., 2019. Using camera traps to study the age-sex structure and behaviour of crop-using elephants Loxodonta africana in Udzungwa Mountains National Park, Tanzania. Oryx 53, 368–376. https://doi.org/10.1017/S0030605317000345

Songhurst, A., McCulloch, G., Coulson, T., 2016. Finding pathways to human-elephant coexistence: A risky business. ORYX 50, 713–720. https://doi.org/10.1017/S0030605315000344

Spiegel, O., Leu, S.T., Bull, C.M., Sih, A., 2017. What's your move? Movement as a link between personality and spatial dynamics in animal populations. Ecol. Lett. 20, 3–18. https://doi.org/10.1111/ele.12708

Stillfried, M., Gras, P., Börner, K., Göritz, F., Painer, J., Röllig, K., Wenzler, M., Hofer, H., Ortmann, S., Kramer-Schadt, S., 2017. Secrets of success in a landscape of fear: Urban wild boar adjust risk perception and tolerate disturbance. Front. Ecol. Evol. 5, 1–12. https://doi.org/10.3389/fevo.2017.00157

Tiller, L.N., Humle, T., Amin, R., Deere, N.J., Lago, B.O., Leader-Williams, N., Sinoni, F.K., Sitati, N., Walpole, M., Smith, R.J., 2021. Changing seasonal, temporal and spatial crop-raiding trends over 15 years in a human-elephant conflict hotspot. Biol. Conserv. 254, 108941. https://doi.org/10.1016/j.biocon.2020.108941

Troup, G., Doran, B., Au, J., King, L.E., Douglas-Hamilton, I., Heinsohn, R., 2020. Movement tortuosity and speed reveal the trade-offs of crop raiding for African elephants. Anim. Behav. 168, 97–108. https://doi.org/10.1016/j.anbehav.2020.08.009

Tucker, M.A., Böhning-Gaese, K., Fagan, W.F., Fryxell, J.M., Van Moorter, B., Alberts, S.C., Ali, A.H., Allen, A.M., Attias, N., Avgar, T., Bartlam-Brooks, H., Bayarbaatar, B., Belant, J.L., Bertassoni, A., Beyer, D., Bidner, L., van Beest, F.M., Blake, S., Blaum, N., et al., 2018. Moving in the Anthropocene: Global reductions in terrestrial mammalian movements. Science 359, 466–469. https://doi.org/10.1126/science.aam9712

Tyrrell, P., Betjes, K., Broekhuis, F., Buitenwerf, R., Hahn, N., Haywood, D., Klaassen, B., Maiyo, C., Mbithi, H., Mwangi, N., Ochola, C., Ondrusek, V., Ratemo, J., Pope, F., Sairowua, W., Sigilai, K., Stabach, J.A., Svenning, J., Stone, E., et al., n.d. Landscape Dynamics (landDX) database: An integrated open-access spatial- temporal database for conservation and rangeland management in the Kenya- Tanzania borderlands. Nat. Sci. Data 1–18.

Veldhuis, M.P., Ritchie, M.E., Ogutu, J.O., Morrison, T.A., Beale, C.M., Estes, A.B., Mwakilema, W., Ojwang, G.O., Parr, C.L., Probert, J., Wargute, P.W., Grant Hopcraft, J.C., Olff, H., 2019. Cross-boundary human impacts compromise the Serengeti-Mara ecosystem. Science (80-.). 363, 1424–1428. https://doi.org/10.1126/science.aav0564

Vogel, S.M., Lambert, B., Songhurst, A.C., McCulloch, G.P., Stronza, A.L., Coulson, T., 2020. Exploring movement decisions: Can Bayesian movement-state models explain crop consumption behaviour in elephants (Loxodonta africana)? J. Anim. Ecol. 1055–1068. https://doi.org/10.1111/1365-2656.13177

Wall, J., Wittemyer, G., Klinkenberg, B., LeMay, V., Blake, S., Strindberg, S., Henley, M., Vollrath, F., Maisels, F., Ferwerda, J., Douglas-Hamilton, I., 2021. Human footprint and protected areas shape elephant range across Africa.

Wittemyer, G., Northrup, J.M., Bastille-Rousseau, G., 2019. Behavioural valuation of landscapes using movement data. Philos. Trans. R. Soc. B Biol. Sci. 374, 20180046. https://doi.org/10.1098/rstb.2018.0046

Woodroffe, R., Thirgood, S., Rabinowitz, A., 2005. People and Wildlife, Conflict or Co-existance? Cambridge University Press, Cambridge. https://doi.org/10.1017/CBO9780511614774

CHAPTER 2: STAGING BEHAVIORS IDENTIFY SPATIAL AND TEMPORAL RISK OF HUMAN-WILDLIFE CONFLICT

Summary

Habitat conversion to farmland has increased human-wildlife interactions that often lead to conflict, injury, or death for people and animals. Understanding the behavioral and landscape drivers of human-wildlife conflict is critical for managing wildlife populations. Staging behavior 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 behavior with opportunities for application to real-time management for conflict prediction. We developed an algorithmic approach based on omission-commission testing to assess the efficacy of six widely used metrics of animal movement to identify staging behavior 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 behavioral 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 algorithms using movement and spatial metrics to predict crop incursions based on GPS data. Our approach identified staging behavior 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 behavioral 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. Our work shows some of the challenges and advantages of using animal behavior to assess temporal and spatial heterogeneity in human-wildlife conflict and demonstrates the need to further incorporate animal movement data into conflict management approaches. Our approach is extendable to

other conflict-prone species to assess pre-conflict behaviors and space use. Fine scale movement data applied to management aims allows targeted and proactive mitigation and can facilitate effective spatial planning.

1. Introduction

Human expansion into wildlife areas and habitat conversion has increased 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 and 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 behavioral 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 behavior, risk of conflict is not static (Laffan et al., 2016). An animal's decision-making during conflict can be driven by risk-reward tradeoffs akin to anti-predation behavior (Frid and 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 and 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 behavior and understanding how temporal and spatial variation in this behavior 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 (Weise et al., 2019).

In many migratory species, staging and stopover sites provide a safe area to avoid predators while resting and refueling during migration (Dingle and Drake, 2007). The choice of stopover location and behavior within these sites is generally the outcome of safety and foraging tradeoffs, 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). Pre-conflict 'staging' behavior 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 is consistently described as confined movement within densely covered habitat during the day in advance of incursions into crops and urban areas at night. As found with migratory staging, it is theorized that staging areas, defined as refuge habitat that animals use to access crops, could provide safety in human-dominated areas and allow animals to remain close 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 and Walpole, 2005; Tiller et al., 2021; Troup et al., 2020). They 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 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 in areas of lower human footprint (Denninger-Snyder et al., 2019; Sitati and Walpole, 2005; Wilson et al., 2015), and elephants may use these forest patches as staging areas to access crop fields (Tiller et al., 2021). Despite recognition of this behavior 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.

We analyzed a long-term GPS elephant movement dataset to investigate the mechanisms and propensity of staging behavior employed during crop raiding by elephants. Our analysis is structured following four objectives. First, we outline and implement an approach to define staging 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 behavior, the implications for proactive management of human-wildlife conflict across species, and directions for future research.

2. Methods

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 km^2. 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 buffered 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 area interface ranges from a hard edge (non-protected crop land adjacent to core areas) to soft edges (limited use areas 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).

Tracking Data

We analyzed GPS data collected from 2011 to 2021 from 55 elephants (185 elephant-years) that have been tracked as part of long-term research projects in Kenya and Tanzania (details in Hahn et al., 2021). GPS data collected from females (n = 27) represent a family unit while males (n = 28) are dispersed and represent a single individual. Locations were filtered to the spatial extent of the study area, subsampled to 1-hour intervals where necessary, and individuals with <95% fix success rates were removed. After cleaning, the dataset totaled 1,054,680 locations. To delineate movement during agricultural use, we defined agricultural use days based on whether elephants used agriculture that day. Because crop use occurs primarily at night, a day for this analysis was the period between 6am and 5am.

Environmental Data

Spatial covariates were compiled to analyze agricultural use and staging locations (Table B2). 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, and defined as areas with over 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-meter SRTM digital elevation model (Farr et al., 2007). Human footprint was assessed using the Google Open Buildings product for Africa, which classifies permanent structures using machine learning (Sirko et al., 2021). Land use status was categorized as core area, limited use, and unprotected (Fig. 5). We used individual elephant-years as the sampling unit for agricultural-use and movement metrics and defined years using an April cutoff to avoid splitting up crop seasons.

Staging Identification

To address our first objective to identify staging behavior prior to agricultural incursions, we used an iterative algorithm and ensemble modeling approach to explore the efficacy of six different movement metrics to detect staging movement patterns: hourly step length, straightness index, tortuosity, net squared displacement, persistence velocity, and hidden Markov model-derived behavioral state (Table 4). We chose these metrics because they have either previously been found to capture differentiated movement behavior in elephants during crop incursions (Hahn et al., 2021; Troup et al., 2020), or were expected to capture embedded movement consistent with previously observed staging behavior.

Based on elephant activity budgets and timing of known crop use (Hahn et al., 2021; Tiller et al., 2021), we explored movement behavior between 6am and 9pm and potential stage lengths within this period from 2 to 16 hours. Using these parameters, the data could be segregated into 120 combinations of possible staging time windows. Within each time window, we calculated the value of the given movement parameter and assessed how well that value combined with the time of day and window size identified staging using omission and commission rates. Commission is defined as the inclusion of non-crop related movement (false positives) and omission is defined as the failure of the algorithm to identify pre-crop movement (false negatives). Algorithm iterations were used to test the parameter space of each metric.

All movement metric calculations and algorithms were run in R version 4.1. Detailed metric definitions and parameterizations can be found in Appendix 2.1.

To create a staging classification based on the many algorithm iterations for each metric, we used weighted majority voting (Punera and Ghosh, 2008) to consolidate iterations based on performance and create a single ensemble classification for each movement metric. Here, we assigned weights to each iteration based on 1-commission error (i.e. lower commission error is weighted higher) (Fig. 6.2). The total weight for each GPS location was calculated as the sum of individual iteration weights, and the location was classified as staging if the weight for a location was greater than the average weight for all possible staging locations. For each movement metric, omission-commission testing was used to evaluate the overall ensemble stage classification and sensitivity to individual differences in elephants.

Spatial and Temporal Drivers of Staging

To investigate our second objective, we assessed how staging events on the landscape were driven by natural and anthropogenic factors. For a given staging 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 (Fig. 6.3). We assumed that staging would not occur in farms and therefore excluded all GPS locations occurring inside agriculture. Environmental covariates were down-sampled and extracted for every pixel in the grid. We used mixed-effects logistic regression with elephant ID as a random effect to assess the propensity to stage, where each pixel value was weighted using the total count of locations for that pixel. To account for spatial autocorrelation, we included an autocovariate based on an inverse weighting scheme, a symmetric neighborhood matrix, and a search radius that was defined dynamically for each elephant grid to select the lowest value at which all points had neighbors (Bardos et al., 2015). We developed biologically realistic candidate models and evaluated all models using corrected Akaike Information Criterion (Burnham et al., 2011). Covariates (percent forest cover, percent agriculture, drainages, slope, and percent permanent buildings) were chosen based on expectations that staging clusters would relate to natural features which provide cover, readily available agriculture, and reduced exposure to human settlements. Because covariate values were measured at different scales, continuous covariates were scaled and centered. Tests for multicollinearity in predictors showed that variance inflation values did not exceed 1.5 for either staging definition. 10-fold cross validation with 5 repeats was used to assess the predictive performance of each model.

To investigate our third objective, we used the identified staging events to investigate movement patterns and timing of staging behavior 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.

Enhancing Predictive Performance of Staging

To address our fourth objective to assess the viability of predicting crop incursions using movement algorithms, we compared our movement-only algorithm to a second algorithm that incorporated spatial agricultural data. Spatial filters that can remove biologically implausible stages (i.e. false-positive locations far away from crops) may be useful for improving omission and commission rates. Agricultural data was added to the algorithm using a spatial threshold to filter out possible staging events based on the distance of a GPS location to agriculture. This spatial threshold was defined as the 95th percentile of Euclidean distance to agriculture during agricultural use days. We applied the omission-commission testing structure to compare the movement-only and spatial threshold algorithm 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

Staging Classification

In our evaluation of algorithm ensemble performance, results varied between all metrics but we found that tortuosity and HMM-derived behavioral state were the most informative in relation to our objectives to predict crop use and investigate spatial drivers of staging. Results for all algorithms can be found in Table B1. Tortuosity produced the best omission rate – 13% failure to identify agricultural use days, with an interquartile range of 9% to 14% between individuals – but performed worse with commission – 49% commission, with IQR of 47% to 58% (Table 4). Behavioral state had a worse omission rate (36%, IQR of 31% to 61% among individuals) but was better with commission (44%, IQR of 42% to 46%) (Table 4). Ensemble classification of staging using tortuosity produced 13,954 staging events occurring between 9am and 6pm, while classification of staging using behavioral state produced 5,928 staging events occurring between 8am and 6pm.

Spatial Drivers of Staging

For our second objective, we evaluated landscape properties of identified staging event locations (Fig. 7a-b). For both staging definitions (tortuosity and behavioral state), the most parsimonious generalized logistic mixed model based on AICc included proportion of forest cover, slope, drainages, proportion of agriculture, and proportion of human settlement (Table B2,B3). The effect size for the proportion of forest cover covariate was the greatest for both tortuosity and behavioral state models, indicating strong selection for forest patches when staging (Table 6). Drainages also had a positive effect in both models. The metrics differed in relation to proportion of agriculture, proportion of human settlement, and slope for which behavioral state staging was more positively correlated (Table 6). Tortuosity-defined staging was more likely to occur in protected and limited use areas compared to unprotected areas, while behavioral state-defined staging was most likely to occur in unprotected areas. Additionally, the autocovariate estimate for the behavioral state model was higher, suggesting that behavioral state-defined staging is more spatially clustered on the landscape. Tortuosity-defined staging appeared to occur predominantly in the Serengeti side of the system, while behavioral state-defined staging occurred more in the Mara (Fig. 7c-d). 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 (1,209 km^2) relative to the area covered by behavioral state staging (307 km^2; Fig. B1). Cross validation indicated that the behavioral state model had more predictive power (root mean squared error = 0.118, mean average error = 0.071) but high variation not explained by the covariates (pearson's R^2 = 0.103). The tortuosity model had lower predictive power (root mean squared error = 0.221, mean average error = 0.187) and slightly less variation (pearson's R^2 = 0.15)

Temporal Drivers of Staging

For our third objective, we assessed daily and seasonal trends in staging occurrence. At the daily scale, elephant movement metrics during agricultural use days showed strong differentiation when staging versus not during the day (Fig. 8a-b). This trend was similar for tortuosity and behavioral state staging definitions. However, assessment of elephant speed during staging revealed that tortuosity staging averaged faster movements during the day than behavioral state staging (Fig. 9). For both metrics, stage length had a mean of 5 hours with an interquartile range of 3 to 7 hours across individuals. At seasonal scales, tortuosity and behavioral state staging occurred more frequently during the transition and dry seasons, although staging also occurred during the wet season (Fig. 10).

Updating staging identification with spatial and temporal filters

To address our fourth objective to test the feasibility of predicting crop incursions from day-time movement and spatial attributes, we created a second algorithm to remove false positive staging events occurring far away from crop fields using a spatial threshold filter of 3.5km for distance to agriculture. This threshold improved commission across both movement metrics. The effect was most pronounced for tortuosity – 30% of staging events were false positives, a decrease of 20% compared to the movement-only results. HMM-defined behavioral state also improved (35% false positive, decrease of 9%) (Table

5). Omission rates for both metrics rose with the spatial filter as it excluded some stages occurring more than 3.5km from agriculture. Overall, tortuosity had the best omission and commission rate of all 6 metrics after adding a spatial threshold for distance to agriculture (Table B1). In a conflict prediction scenario, the algorithm using tortuosity and distance to agriculture would produce an average of 3,419 alarms per year, with 480 false alarms and 274 missed alarms, while the behavioral state spatial threshold algorithm would produce 1,257 alarms per year, with 570 false alarms and 624 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 (Mukeka 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 behavior and space use leading up to conflict are limited (Blackwell et al., 2016). Staging behavior 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 behavior prior to agricultural incursions from GPS tracking data using African elephants and six movement metrics (tortuosity and hidden Markov model-derived behavioral states being the most explanatory) as a case study. These metrics highlighted different aspects of staging behavior that, ultimately, may be useful in addressing different objectives for managing human-elephant interactions. Specifically, the behavioral states application highlighted spatially constrained staging events described elsewhere (Tiller et al. 2021), while tortuosity-based staging captured a spatially dispersed meandering behavior prior to agricultural incursions that occurred more within protected areas. In contrast to our assumption of staging being highly embedded, tortuosity-based staging was more pronounced (in terms of propensity) and wide-spread (in terms of area where it occurred) in the study system.

Our results highlight considerable spatial heterogeneity in both the level and type of conflict risk and the ability of elephants to adapt their movement strategies depending on the landscape. While our algorithm approach was able to proactively identify agricultural use on a majority of days, the omission rates across all movement metrics suggest that missed events are likely due to a variety of non-staging pre-crop strategies that elephants employ, rather than a failure to identify staging. Overall, behavioral state-defined staging occurred on a smaller subset of agricultural use days, but was highly spatially clustered in the system and highly predictable in relation to spatial covariates, which we assume would make it most useful for identifying and targeting specific areas on the landscape for landscape planning approaches. Tortuosity staging occurred on a vast majority of agricultural use days, was dispersed throughout the study area, was the most reliable predictor of agricultural use based on commission and omission errors, but was harder to predict in relation to spatial covariates. We assume that these traits may be most useful for prediction of agricultural incursions from GPS movement data, rather than applying directly towards landscape planning efforts.

The distinction in both movement and environmental correlates for staging defined using tortuosity and behavioral state appeared to be linked to gradients in the juxtaposition between fully 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 the study system only allow tourism, meaning elephant behavior in such areas was less inhibited by human interaction. In contrast, behavioral state-defined staging events occurred more often in limited use areas (e.g. community conservancies) in the Mara ecosystem and unprotected land, which are prone to regular livestock grazing and human activity during the day. In such areas, elephants reduced their movements and sought staging areas with greater cover habitat. Overall, the encamped 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).

In our assessment of staging at seasonal scales, staging was more common during the transition and dry season relative to the wet season. These are typically the seasons with the highest rates of conflict as natural vegetation browns down and crops ripen (Denninger-Snyder et al., 2019; Tiller et al., 2021). However, we were surprised to detect staging during the wet season, when fields are generally fallow or at seedling stages. These field incursions indicate that staging may provide multiple benefits not exclusive to crop use, such as access to desirable resources outside protected areas and for range expansion during the wet season (Tiller, 2017), and helps explain the consistently higher false positive rates during the wet season.

The definition of wildlife movement behaviors that can identify pre- crop raiding behavior 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. If identified hotspots are widely used, such spatio-temporal management action can potentially impact non-collared crop-raiders. In addition, spatial attributes of staging could be used towards agricultural plot-level mitigation schemes, such as planting of unpalatable buffer crops and alternative income programs (Chang'a et al., 2016). In this system, areas with relatively more behavioral state-defined staging areas would be most suited to these approaches (Fig. 7).

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 commission while keeping omission rates 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 behavior. After definition, real time application of the defined metric can be applied to enable proactive management intervention. Alternatively, machine learning approaches that can be trained over time to more accurately identify movement of management relevance (like staging) may be a promising approach to pursue building off the lessons from the type of analysis presented here (Wang, 2019).

Understanding the complexity of conflict behaviors 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 behavior, the algorithmic approach is translatable to other species that have been described employing such behaviors (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 that are already monitored, in ecosystems with landscape traits that appear to drive staging, areas with planned buffer zones or corridors that may facilitate staging, or where climate change is expected to shift conflict risk (Bautista et al., 2021; Kitratporn and Takeuchi, 2022; Lewis et al., 2015). Such investigations can play a pivotal role in motivating mitigation efforts and informing land use planning initiatives that incorporate behavioral complexity into human-wildlife conflict risk.

5. Tables & Figures

Table 4. The movement metrics tested to define staging behavior. All metrics are calculated for the track segment in each time window (n = 120).

Metric	**Definition**	**Expected relationship to staging**	**Reference**
Mean Step size/length	The mean displacement within the time window	Lower	Seidel et al., 2018
Straightness Index	The ratio of net displacement R to total path segment length L; log(R/L)	Lower	Benhamou, 2004
Tortuosity	The ratio of total 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 within the time window	Lower	Seidel et al., 2018
Persistence Velocity	The mean of the speed of movement in the direction of heading; speed*cos(absolute turning angle)	Lower	Seidel et al., 2018
HMM Behavioral State	Percentage of encamped GPS fixes	Higher	Hahn et al., 2022

Table 5. Omission-commission results from ensemble algorithm outputs. Omission is the percentage of agricultural use days that were not detected using the staging algorithm (false negative). Commission is the percentage of non-agricultural use days that were classified as agricultural stages by the algorithm (false positive). Values are reported as percentages.

Metric	**Type**	**Movement Only**	**Ag Filter**
HMM Behavioral State	Omission	0.36	0.37
	Commission	0.44	0.35
Tortuosity	Omission	0.13	0.17
	Commission	0.51	0.3

Table 6. Generalized logistic mixed models for environmental predictors of staging areas using the behavioral state and tortuosity metrics. Coefficient estimates and 95% confidence intervals are reported on the log odds scale. 95% confidence intervals for tortuosity and behavioral 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.

	Tortuosity		**HMM Behavioral State**	
Coefficient	**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	$s^2_{ID} = 0.09$		$s^2_{ID} = 0.26$	

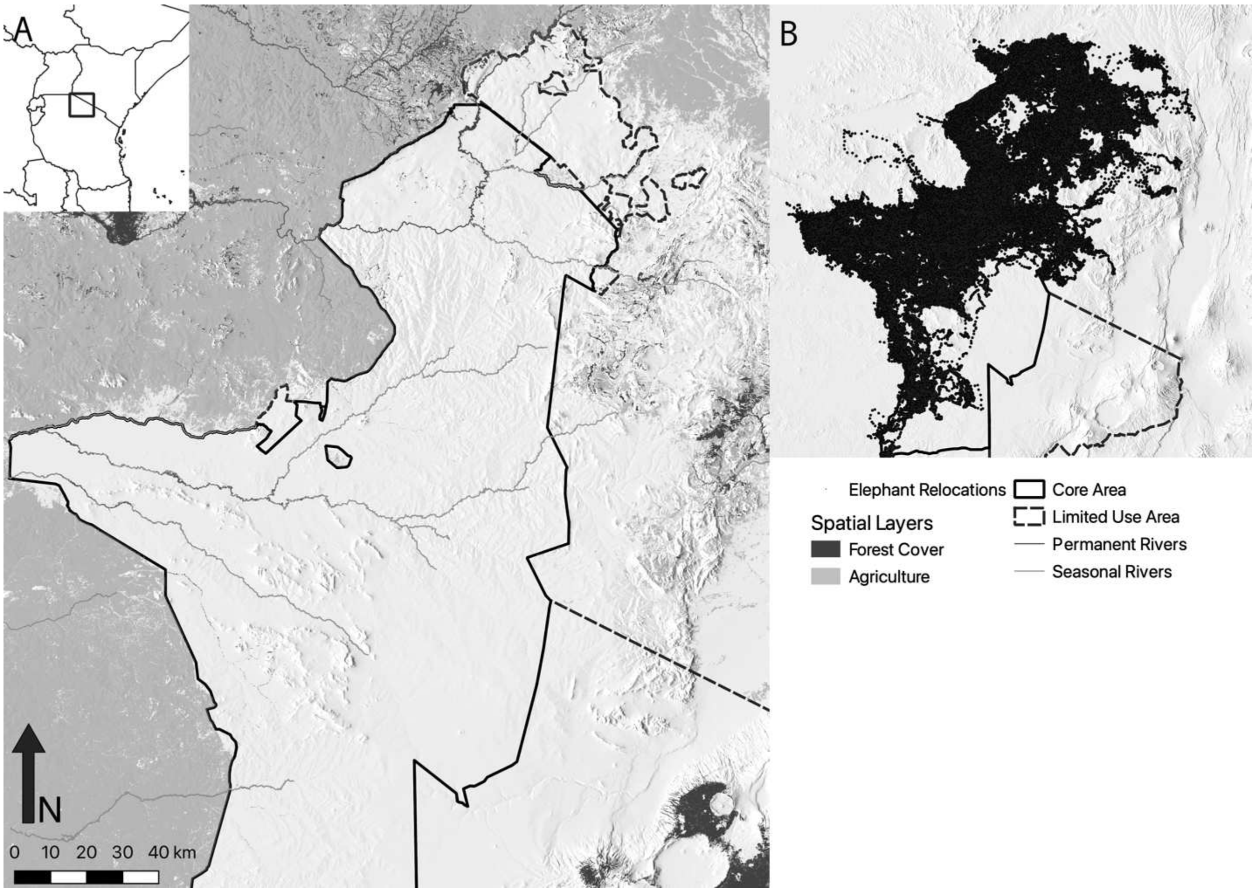

Figure 5. A) The Greater Serengeti-Mara Ecosystem showing core and limited use protected areas, agriculture, forest, permanent and seasonal rivers, and topography. Protected area boundaries have been simplified. B) Shows the GPS relocations of the 55 individuals included in the study.

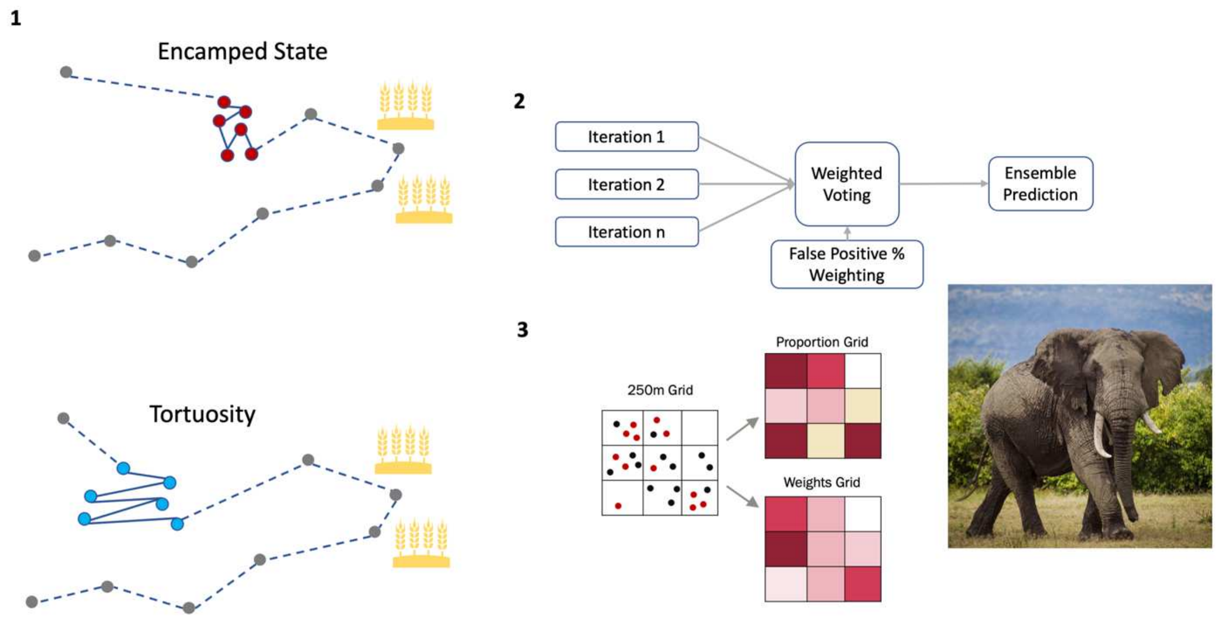

Figure 6. An example workflow for ensemble classification and spatial modeling of staging events from GPS data using the percentage of encamped behavioral state steps. The workflow follows 3 steps: 1) The movement track is scanned for staging events considering staging length, time of day, and a threshold value for the staging metric. 2) For each movement metric, the results of the individual algorithm iterations are combined using weighted voting to produce an ensemble classification of staging events. 3) From the tagged staging events, the occurrence of staging in relation to natural and human footprint variables can be assessed using a weighted spatial regression. Staging occurrence is quantified using the proportion of staging to non-staging locations on a 250m grid.

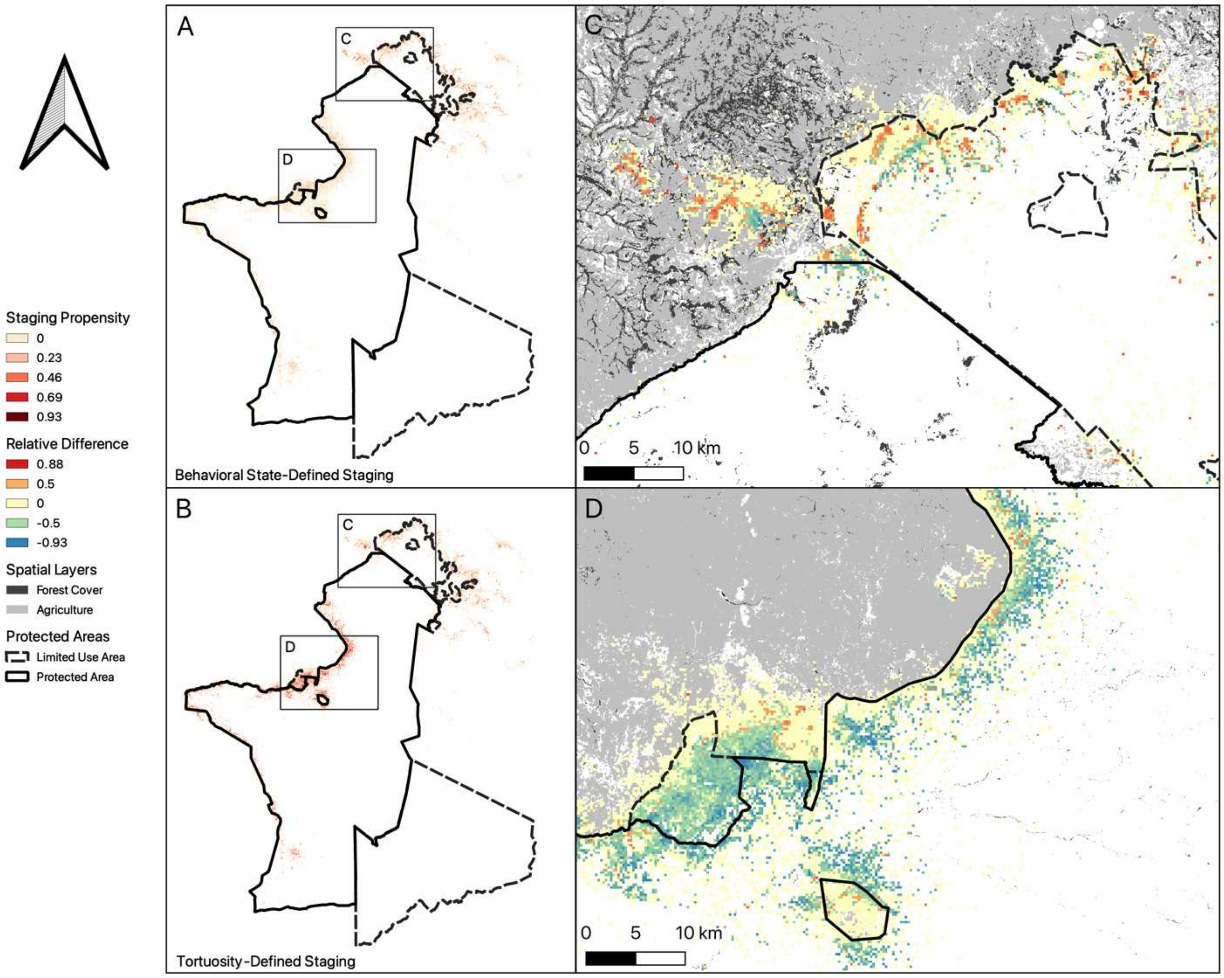

Figure 7. A comparison of staging clusters produced by tortuosity and behavioral state definitions in the Serengeti-Mara System. Panels A and B show HMM-derived behavioral state and tortuosity-defined staging propensity values, respectively. Darker reds indicate areas of greater staging propensity (ratio of staging to non-staging use). C and D show the relative difference in cell values between the tortuosity and behavioral state defined events in a section of the Mara region (C) and the western Serengeti (D). Warmer colors (positive values) indicate cells with more behavioral state staging and cooler colors (negative values) indicate cells with more tortuosity-based staging. Note the greater proportion of HMM-behavioral state events in the limited use areas and the opposite contrast in the protected areas.

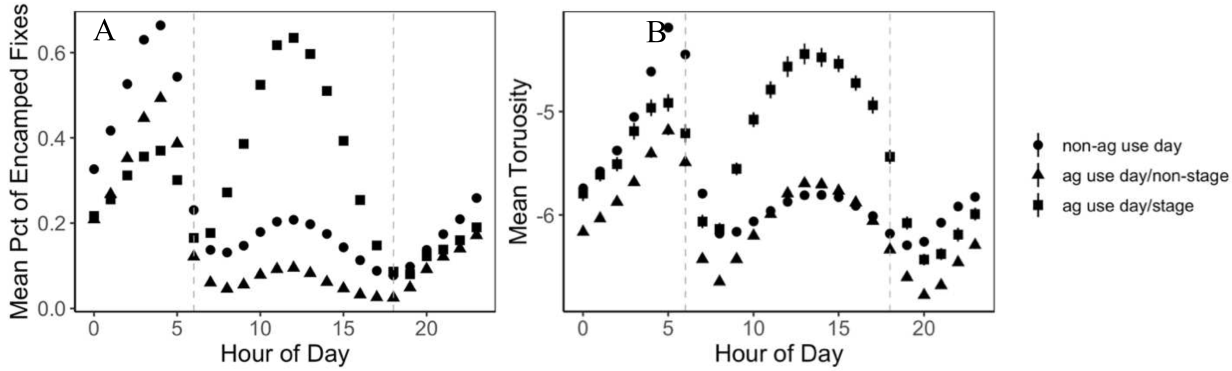

Figure 8. Hourly activity budgets are shown for agricultural use days with staging days (squares), agricultural use non-staging days (triangles), and non-agricultural use days (circles), and highlight the reduction in daytime movement during staging events. Budgets are calculated for each individual and bars represent 95% confidence intervals. (A) shows the mean staging propensity defined using tortuosity for each hour among all elephants. (B) shows the mean staging propensity defined as encamped relocations for each hour among all elephants. Grey dashed lines indicate approximate sunrise (6am) and sunset (6pm).

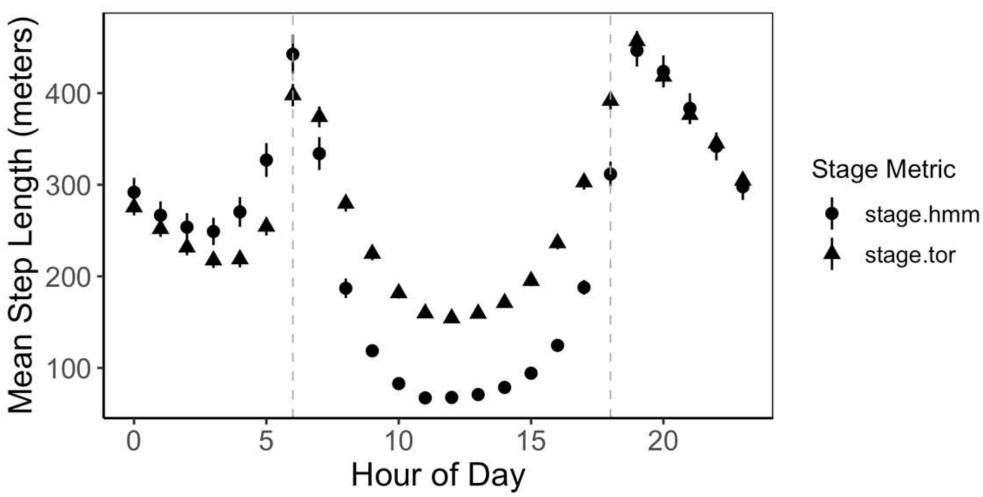

Figure 9. Mean hourly step length for days with HMM-behavioral state (circles) and tortuosity (triangles) defined staging events, highlighting that events identified using behavioral states show notably lower displacement relative to those identified using tortuosity. The mean step lengths are calculated by individual, and bars correspond to 95% confidence intervals. Grey dashed lines indicate approximate sunrise (6am) and sunset (6pm).

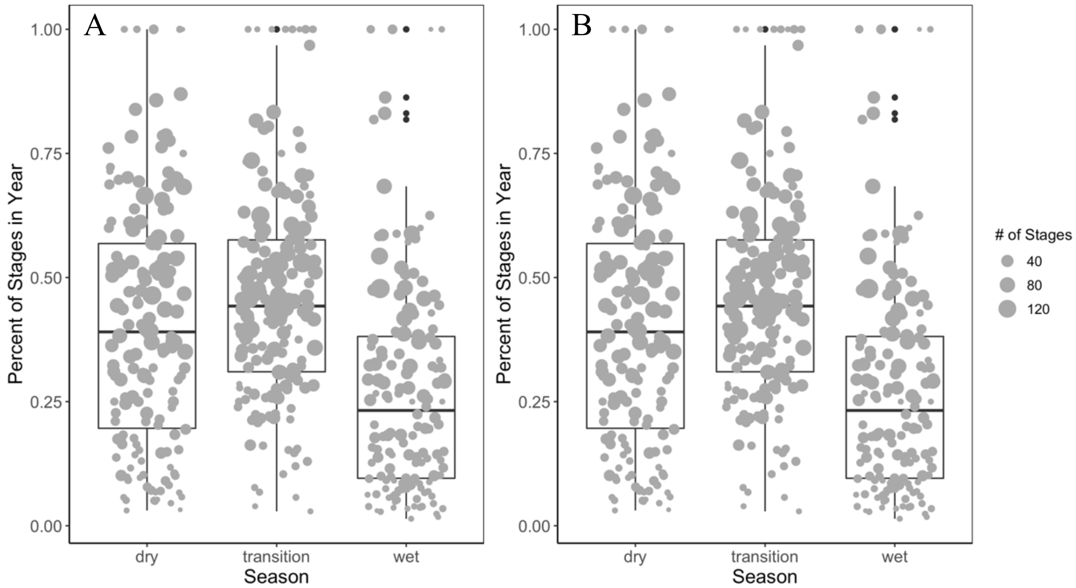

Figure 10. Seasonal trends in staging are shown for A) the tortuosity metric and B) the HMM-behavioral state metric showing the propensity for staging to occur during drier periods in the study areas. Boxplots show the percent of agricultural use days with a stage occurring within each season. Overlayed points show the calculated percentages for 205 elephant-years. The size of the points corresponds to the number of stages by an individual in a given year for tortuosity (max = 158) and behavioral state (max = 127).

6. References

Bardos, D.C., Guillera-Arroita, G., Wintle, B.A., 2015. Valid auto-models for spatially autocorrelated occupancy and abundance data. Methods Ecol. Evol. 6, 1137–1149. https://doi.org/10.1111/2041-210X.12402

Bastille-Rousseau, G., Wall, J., Douglas-Hamilton, I., Lesowapir, B., Loloju, B., Mwangi, N., Wittemyer, G., 2020. Landscape-scale habitat response of African elephants shows strong selection for foraging opportunities in a human dominated ecosystem. Ecography (Cop.). 43, 149–160. https://doi.org/10.1111/ecog.04240

Bautista, C., Revilla, E., Berezowska-Cnota, T., Fernández, N., Naves, J., Selva, N., 2021. Spatial ecology of conflicts: Unravelling patterns of wildlife damage at multiple scales. Proc. R. Soc. B Biol. Sci. 288. https://doi.org/10.1098/rspb.2021.1394

Benhamou, S., 2004. How to reliably estimate the tortuosity of an animal's path: Straightness, sinuosity, or fractal dimension? J. Theor. Biol. 229, 209–220. https://doi.org/10.1016/j.jtbi.2004.03.016

Blackwell, B.F., DeVault, T.L., Fernández-Juricic, E., Gese, E.M., Gilbert-Norton, L., Breck, S.W., 2016. No single solution: application of behavioural principles in mitigating human–wildlife conflict. Anim. Behav. 120, 245–254. https://doi.org/10.1016/j.anbehav.2016.07.013

Branco, P.S., Merkle, J.A., Pringle, R.M., Pansu, J., Potter, A.B., Reynolds, A., Stalmans, M., Long, R.A., 2019. Determinants of elephant foraging behaviour in a coupled human-natural system: Is brown the new green? J. Anim. Ecol. https://doi.org/10.1111/1365-2656.12971

Broekhuis, F., Cushman, S.A., Elliot, N.B., 2017. Identification of human–carnivore conflict hotspots to prioritize mitigation efforts. Ecol. Evol. 7, 10630–10639. https://doi.org/10.1002/ece3.3565

Burnham, K.P., Anderson, D.R., Huyvaert, K.P., 2011. AIC model selection and multimodel inference in behavioral ecology: Some background, observations, and comparisons. Behav. Ecol. Sociobiol. https://doi.org/10.1007/s00265-010-1029-6

Chang'a, A., de Souza, N., Muya, J., Keyyu, J., Mwakatobe, A., Malugu, L., Ndossi, H.P., Konuche, J., Omondi, R., Mpinge, A., Hahn, N., Palminteri, S., Olson, D., 2016. Scaling-up the use of chili fences for reducing human-elephant conflict across landscapes in Tanzania. Trop. Conserv. Sci. 9, 921–930. https://doi.org/10.1177/194008291600900220

Denninger-Snyder, K., Mneney, P., Benjamin, B., Mkilindi, P., Mbise, N., 2019. Seasonal and spatial vulnerability to agricultural damage by elephants in the western Serengeti, Tanzania. Oryx 1–11. https://doi.org/10.1017/S0030605318001382

Dickman, A.J., 2010. Complexities of conflict: The importance of considering social factors for effectively resolving human-wildlife conflict. Anim. Conserv. 13, 458–466. https://doi.org/10.1111/j.1469-1795.2010.00368.x

Dingle, H., Drake, V.A., 2007. What Is Migration? Bioscience 57, 113–121. https://doi.org/10.1641/B570206

Fang, F., Tambe, M., Dilkina, B., Plumptre, A.J. (Eds.), 2019. Artificial Intelligence and Conservation, Artificial Intelligence and Conservation. Cambridge University Press. https://doi.org/10.1017/9781108587792

Farr, T.G., Rosen, P.A., Caro, E., Crippen, R., Duren, R., Hensley, S., Kobrick, M., Paller, M., Rodriguez, E., Roth, L., Seal, D., Shaffer, S., Shimada, J., Umland, J., Werner, M., Oskin, M., Burbank, D., Alsdorf, D.E., 2007. The shuttle radar topography mission. Rev. Geophys. https://doi.org/10.1029/2005RG000183

Frid, A., Dill, L., 2002. Human-caused disturbance stimuli as a form of predation risk. Ecol. Soc. 6. https://doi.org/10.5751/es-00404-060111

Goswami, V.R., Vasudev, D., 2017. Triage of Conservation Needs: The Juxtaposition of Conflict Mitigation and Connectivity Considerations in Heterogeneous, Human-Dominated Landscapes. Front. Ecol. Evol. 4, 144. https://doi.org/10.3389/fevo.2016.00144

Grill, G., Lehner, B., Thieme, M., Geenen, B., Tickner, D., Antonelli, F., Babu, S., Borrelli, P., Cheng, L., Crochetiere, H., Ehalt Macedo, H., Filgueiras, R., Goichot, M., Higgins, J., Hogan, Z., Lip, B., McClain, M.E., Meng, J., Mulligan, M., et al., 2019. Mapping the world's free-flowing rivers. Nature 569, 215–221. https://doi.org/10.1038/s41586-019-1111-9

Hahn, N.R., Wall, J., Denninger-Snyder, K., Goss, M., Sairowua, W., Mbise, N., Estes, A.B., Ndambuki, S., Mjingo, E.E., Douglas-Hamiliton, I., Wittemyer, G., 2021. Risk perception and tolerance shape variation in agricultural use for a transboundary elephant population. J. Anim. Ecol. 91, 112–123. https://doi.org/10.1111/1365-2656.13605

Hansen, M.C., Potapov, P. V., Moore, R., Hancher, M., Turubanova, S.A., Tyukavina, A., Thau, D., Stehman, S. V., Goetz, S.J., Loveland, T.R., Kommareddy, A., Egorov, A., Chini, L., Justice, C.O., Townshend, J.R.G., 2013. High-resolution global maps of 21st-century forest cover change. Science (80-.). https://doi.org/10.1126/science.1244693

Kitratporn, N., Takeuchi, W., 2022. Human-elephant conflict risk assessment under coupled climatic and anthropogenic changes in Thailand. Sci. Total Environ. 834, 155174. https://doi.org/10.1016/j.scitotenv.2022.155174

König, H.J., Kiffner, C., Kramer-Schadt, S., Fürst, C., Keuling, O., Ford, A.T., 2020. Human–wildlife coexistence in a changing world. Conserv. Biol. 34, 786–794. https://doi.org/10.1111/cobi.13513

Laffan, S.W., Skidmore, A.K., Franklin, J., 2016. Space, time, connectivity and conflict in biological landscapes: the fourth special issue on spatial ecology. Int. J. Geogr. Inf. Sci. 30, 1–4. https://doi.org/10.1080/13658816.2015.1090001

Lewis, D.L., Baruch-Mordo, S., Wilson, K.R., Breck, S.W., Mao, J.S., Broderick, J., 2015. Foraging ecology of black bears in urban environments: Guidance for human-bear conflict mitigation. Ecosphere 6, 1–18. https://doi.org/10.1890/ES15-00137.1

Marchinton, F.B., 1995. Movement Ecology of Black Bears in a Fragmented Bottomland Hardwood Habitat in Louisiana. University of Tenessee, Knoxville.
Mekonnen, A., Bekele, A., Fashing, P.J., Lernould, J.-M., Atickem, A., Stenseth, N.C., 2012. Newly Discovered Bale Monkey Populations in Forest Fragments in Southern Ethiopia: Evidence of Crop Raiding, Hybridization With Grivets, and Other Conservation Threats. Am. J. Primatol. 74, 423–432. https://doi.org/10.1002/ajp.21999
Miller, J.R.B., 2015. Mapping attack hotspots to mitigate human–carnivore conflict: approaches and applications of spatial predation risk modeling. Biodivers. Conserv. 24, 2887–2911. https://doi.org/10.1007/s10531-015-0993-6
Miller, J.R.B., Schmitz, O.J., 2019. Landscape of fear and human-predator coexistence: Applying spatial predator-prey interaction theory to understand and reduce carnivore-livestock conflict. Biol. Conserv. 236, 464–473. https://doi.org/10.1016/j.biocon.2019.06.009
Mukeka, J.M., Ogutu, J.O., Kanga, E., Røskaft, E., 2019. Human-wildlife conflicts and their correlates in Narok County, Kenya. Glob. Ecol. Conserv. 18, e00620. https://doi.org/10.1016/j.gecco.2019.e00620
Pomeroy, A.C., Acevedo Seaman, D.A., Butler, R.W., Elner, R.W., Williams, T.D., Ydenberg, R.C., 2008. Feeding-Danger Trade-Offs Underlie Stopover Site Selection by Migrants. Avian Conserv. Ecol. 3. https://doi.org/10.5751/ace-00240-030107
Punera, K., Ghosh, J., 2008. Consensus-based ensembles of soft clusterings. Appl. Artif. Intell. 22, 780–810. https://doi.org/10.1080/08839510802170546
Seidel, D.P., Dougherty, E.R., Carlson, C.J., Getz, W.M., Seidel, D.P., Carlson, C.J., Spiegel, O., Getz, W.M., Dougherty, E.R., Carlson, C.J., Getz, W.M., 2018. Ecological metrics and methods for GPS movement data. Int. J. Geogr. Inf. Sci. 32, 2272–2293. https://doi.org/10.1080/13658816.2018.1498097
Shaffer, L.J., Khadka, K.K., Van Den Hoek, J., Naithani, K.J., 2019. Human-Elephant Conflict: A Review of Current Management Strategies and Future Directions. Front. Ecol. Evol. 6, 235. https://doi.org/10.3389/fevo.2018.00235
Sirko, W., Kashubin, S., Ritter, M., Annkah, A., Bouchareb, Y.S.E., Dauphin, Y., Keysers, D., Neumann, M., Cisse, M., Quinn, J., 2021. Continental-Scale Building Detection from High Resolution Satellite Imagery 1–15.
Sitati, A.N.W., Walpole, M.J., 2005. Factors Affecting Susceptibility of Farms to Crop Raiding by African Elephants : Using a Predictive Model to Mitigate Conflict. J. Appl. Ecol. 42, 1175–1182. https://doi.org/10.1111/j.1365-2664.2005.01091.x
Tiller, L.N., 2017. Understanding how land-use change in the Trans Mara District, Kenya is driving human-elephant conflict and elephant movement. Kent Acad. Repos. University of Kent.
Tiller, L.N., Humle, T., Amin, R., Deere, N.J., Lago, B.O., Leader-Williams, N., Sinoni, F.K., Sitati, N., Walpole, M., Smith, R.J., 2021. Changing seasonal, temporal and spatial crop-raiding trends over 15 years in a human-elephant conflict hotspot. Biol. Conserv. 254, 108941. https://doi.org/10.1016/j.biocon.2020.108941
Troup, G., Doran, B., Au, J., King, L.E., Douglas-Hamilton, I., Heinsohn, R., 2020. Movement tortuosity and speed reveal the trade-offs of crop raiding for African elephants. Anim. Behav. 168, 97–108. https://doi.org/10.1016/j.anbehav.2020.08.009
Veldhuis, M.P., Ritchie, M.E., Ogutu, J.O., Morrison, T.A., Beale, C.M., Estes, A.B., Mwakilema, W., Ojwang, G.O., Parr, C.L., Probert, J., Wargute, P.W., Grant Hopcraft, J.C., Olff, H., 2019. Cross-boundary human impacts compromise the Serengeti-Mara ecosystem. Science (80-.). 363, 1424–1428. https://doi.org/10.1126/science.aav0564
Wang, G., 2019. Machine learning for inferring animal behavior from location and movement data. Ecol. Inform. 49, 69–76. https://doi.org/10.1016/j.ecoinf.2018.12.002
Weise, F.J., Hauptmeier, H., Stratford, K.J., Hayward, M.W., Aal, K., Heuer, M., Tomeletso, M., Wulf, V., Somers, M.J., Stein, A.B., 2019. Lions at the Gates: Trans-disciplinary Design of an Early

Warning System to Improve Human-Lion Coexistence. Front. Ecol. Evol. 6, 242. https://doi.org/10.3389/fevo.2018.00242

Whittington, J., St. Clair, C.C., Mercer, G., 2004. Path tortuosity and the permeability of roads and trails to wolf movement. Ecol. Soc. 9. https://doi.org/10.5751/ES-00617-090104

Wilson, S., Davies, T.E., Hazarika, N., Zimmermann, A., 2015. Understanding spatial and temporal patterns of human-elephant conflict in Assam, India. Oryx 49, 140–149. https://doi.org/10.1017/S0030605313000513

Woodroffe, R., Thirgood, S., Rabinowitz, A., 2005. People and Wildlife, Conflict or Co-existance? Cambridge University Press, Cambridge. https://doi.org/10.1017/CBO9780511614774

CHAPTER 3: CROP USE STRUCTURES RESOURCE SELECTION STRATEGIES IN A HUMAN-DOMINATED LANDSCAPE

Summary

To conserve wide-ranging species in human-modified landscapes it is essential to understand how animals respond to degrees of modification and in turn how this impacts populations. Of widespread interest is wildlife use of agriculture lands that often leads to conflict. Evidence for some species suggests that large inter-individual variation exists in the propensity for conflict, and that this may be driven by both behavioral and landscape factors. Less understood is the impact of crop use on foraging behavior. Research in the Mara-Serengeti Ecosystem of East Africa has shown that elephant space use is highly structured by human activity and that the population is structured by the degree to which individuals' crop-raid. Following these findings, we analyzed GPS data from 56 free-ranging elephants within an ecosystem containing low and high levels of fragmentation to assess how crop use may drive patterns of resource selection and space use within a population. We found wide variation in resource selection coefficient values between individuals, indicating strongly differentiated resource selection strategies across individuals, years, and seasons. Variation was particularly marked during the wet season across years, but individuals were more likely to use a similar strategy in the dry season. Cluster analysis of individual resource selection coefficients indicated they were structured primarily by the degree of crop use in the dry season and time spent in protected and unprotected areas. While crops were avoided at the home range level, controlling for space revealed that crop selection patterns were strongly spatially structured and related to the level of fragmentation. In areas with high fragmentation, large farms and small forest refuges, elephants selected most strongly for areas within 1000m of the protected area boundary. In contrast, elephants selected most strongly for areas 1000-2000m away in areas with low fragmentation, smaller farms, and larger forest refuges. Our results highlight how variation in behavioral responses to human development and landscape change structure resource selection and space use, and by extension population distributions. Our approach can be applied to other species and systems to

characterize individual variation in human resource use and inform mitigations for human-wildlife coexistence.

1. Introduction

Animal movement, dispersal, and habitat selection are important determinants of the spatial distribution and dynamics of wildlife populations in heterogenous landscapes (Lima and Zollner, 1996). In agricultural landscapes, behavioral responses to rapid landscape changes are often driven by foraging tradeoffs in accessing highly nutritious resources while reducing risk from humans (Branco et al., 2019; Simon and Fortin, 2019). The way that animals respond to these tradeoffs can structure ecological processes such as predation, reproduction, and intraspecies competition (Robertson et al., 2013; Sih et al., 2011). To survive in agricultural landscapes animals typically alter their movement behavior as resource availability and risk changes (Broekhuis et al., 2019; Paton et al., 2017), which can structure overall shifts in population distributions (Simon and Fortin, 2019; Veldhuis et al., 2019). The juxtaposition of wildlands and human dominated areas also influences animal behavior and space use, such as through the relationship between fragmentation and a species' movement capabilities that can dictate dispersal (Doherty and Driscoll, 2018; Ricketts et al., 2017). The influence of both behavior and landscape on animal movement is of increasing interest, particularly in relation to determining drivers of human-wildlife conflict and wildlife responses to human disturbance (Blackwell et al., 2016; Songhurst et al., 2016). Understanding the fundamental links between landscape fragmentation and its impact on a species' resource requirements and space use is important for designing conservation and management strategies in agricultural landscapes.

Land use change from humans have introduced novel resources and altered the risk landscape for wildlife (Gaynor et al., 2019; Simon and Fortin, 2019). For example, crops represent novel, high-quality food for herbivores but come at the cost of increased mortality risk (Simon and Fortin, 2019; Sukumar and Gadgil, 1988). Crop use by wildlife is a spatially explicit behavior that is thought to be driven by risk-reward tradeoffs as animals employ movement strategies such as moving faster, changing daily activity budgets, and shifting space use to access crops (Branco et al., 2019; Lewis et al., 2015; Troup et al., 2020). Less understood is the foraging tradeoffs that animals make to seek out crops and the extent to which crop use structures space use in a population (Pozo et al., 2018).

The ability to collect detailed longitudinal movement data offers powerful insight for the study of spatially structed behaviors (Joly, 2019), such as human-wildlife interactions (Johnson et al., 2015). Resource-selection functions (RSFs), which compare landscape characteristics at used sites to those at random sites, can be a valuable research tool to study foraging strategies within a population (Leclerc et al., 2016; Sawyer et al., 2006). More recently, interest has grown in using inter- and intra-individual variation in resource selection to understand drivers of population distribution and key areas on the landscape for population persistence (Bastille-Rousseau et al., 2019; Wittemyer et al., 2019). Relating individual heterogeneity in space use to ecological contexts that favor certain tactics or the extent to which individuals can adjust to human pressures can provide further perspective on how tactics may impact population-level responses to environmental change (Spiegel et al., 2017). Although it can be difficult to discern environmental contexts from remotely collected movement data, spatially explicit behaviors such as crop raiding are identifiable (Hahn et al., 2021).

Crop raiding by elephants is one of the most common types of human-wildlife conflict in Africa and Asia, and is rapidly increasing as cultivated land expands near protected areas (Shaffer et al., 2019). Temporally, elephants typically crop-raid at night when they are less likely to be detected (Sitati and Walpole, 2005; Tiller et al., 2021; Troup et al., 2020), and in the dry season when crops mature (Branco et al., 2019). The spatial distribution of humans and wildlife can affect the occurrence and intensity of this conflict, but studies have mainly been limited to assessing where conflict events occur on the landscape without information on wider space use surrounding conflict behavior. Conflict hotspots occur further from human settlements (Denninger-Snyder et al., 2019), and elephants may also use landscape features such as forest patches and drainages to access crops (Pittiglio et al., 2014; Tiller, 2017). However, general elephant space use is not necessarily linked to conflict hotspots (Pozo et al., 2018) and elephants are thought to shift their ranges closer to crops when raiding depending on the landscape structure (Hahn et al., In Review). While resource selection studies that can link crop use to overall foraging strategies, seasonal factors, and sex may be valuable to understand how conflict is influenced by behavioral and landscape factors, this approach has been underserved (Mumby and Plotnik, 2018) (but see Branco et al., 2019).

Previous research on a subset of this population has shown that management zones and the level of protection has strong effects on resource selection, and these effects interact with time of day, season, and sex (Wall et al., In Review). In particular, selection in the unprotected areas is strongly differentiated between wet and dry seasons and time of day, suggesting that crop use and human activity may be a key driver in resource selection strategies. Additionally, analyses in this system have demonstrated that the population is structured by the degree to which individuals crop-raid, allowing subdivision of these individuals into four behavioral tactics around agricultural use (Hahn et al., 2021). Here we build on this insight to (1) quantify the extent to which using crops impacts overall resource selection strategies and (2) assess how the spatial distribution of crop use relates to the interface between natural and crop land. Specifically, we test the hypothesis that crop use necessitates different selection strategies such that elephants that use similar amounts of crops each year and season should have more similar resource selection trends to each other. Further, we test the hypothesis that the amount of crops and level of fragmentation outside protected areas affects crop use such that more farms and more forest cover will result in selection for crops close but not far from protected area edges while fewer farms and more forest cover will result in selection for crops further from protected area edges. We discuss our findings in the context of possible implications on population distributions and conflict risk, management of human-wildlife conflict across species, and directions for future research.

2. Methods

Study Area

The study took place in the Serengeti-Mara Ecosystem, a savannah ecosystem in southwestern Kenya and northwestern Tanzania that spans over 40,000 km2. Vegetation ranges from large grasslands to woodland, bushland thickets, and afro-montane forests. The protected areas in the system are made up of the Serengeti National Park in Tanzania and the Masai Mara National Reserve in Kenya, along with community-managed conservancies and communal lands with managed livestock grazing and no farming (Fig. 11). The remaining area is unprotected, comprised of private and community land used mainly for crops and pastoralism. Agriculture is primarily rain-fed grain crops and is generally planted in the wet season and becomes mature and is harvested during the dry season. Human-elephant conflict is highest after crops mature, but incidences of conflict have generally risen over the last two decades (Mukeka et al., 2019; Tiller et al., 2021). The Mara region is generally less degraded outside protected areas, with crops making up 20.6% of unprotected land compared to 46.9% in the Serengeti. Landscape indices of edge density and contagion index of the unprotected land suggest considerably less fragmentation and more interspersion of natural patches in the Mara (edge density = 161, contagion index = 44.5) compared to the Serengeti (edge density = 217, contagion index = 25.4). To aid in the interpretation of results, we considered the Mara region to represent a soft edge between natural and crop land with low fragmentation, and the Serengeti region to represent a hard edge with high fragmentation.

Tracking Data

We analyzed GPS data collected from 2011 to 2021 from 56 elephants (180 elephant-years) that have been tracked as part of long-term research projects in Kenya and Tanzania (details in Hahn et al., 2021). GPS data collected from females (n = 28) represent a family unit while males (n = 28) are dispersed and represent a single individual. Locations were filtered to the spatial extent of the study area, subsampled to 1-hour intervals where necessary, and individuals with <95% fix success rates were removed. To assess resource selection across seasons, data on individuals was split into elephant-year-seasons (n = 334; 178

dry and 156 wet). Due to our focus on crop selection, we also removed tracking data from elephant-year-seasons that did not interact with crops (4 dry, 2 wet). After cleaning, the dataset totaled 1,244,111 locations.

Environmental Data

Spatial covariates were compiled to analyze resource selection. Land cover was derived from a 10-m Sentinel land cover classification of the Serengeti-Mara ecosystem published in Wall et al., In Review. Natural landcover classes based on the percentage of grass and canopy cover. Overall, landcover classes consisted of bare ground, grassland/savannah, open woodland/bushland, forest/bush thicket, and crops. 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 determine the coefficient of variation in NDVI for each season-year. NDVI values were also used to delineate wet and dry seasons 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 hourly mean step length for elephants. Slope was calculated based on the 30-meter SRTM digital elevation model (Farr et al., 2007). Settlements were assessed using the Google Open Buildings product for Africa, which classifies permanent structures using machine learning (Sirko et al., 2021). We only included buildings with a confidence level greater than 70% and calculated settlement density using a window size of 250m corresponding to mean hourly step length of elephants. Roads (Tyrrell et al., 2022) were categorized into primary and secondary roads, and the Euclidean distance to each road type was calculated as a raster with 10m resolution. The distance to protected area edges was calculated similarly, while allowing for negative values inside of the protected areas.

Resource Selection Functions

To evaluate elephant resource selection relative to crops, we used third-order resource selection functions (RSFs) based on a use-available design (Boyce et al., 2002). To characterize availability for each individual-year-season, we used GPS locations to home ranges using 95% minimum convex polygons and generated random locations representing availability within each polygon. The ratio of available to observed points can affect resource selection function results, so we tested ratios from 20:1 to 50:1 on a subset of individuals and found that model estimates stabilized at 30:1 (Northrup et al., 2013). Available locations were randomly assigned a date and time based on the distribution of the observed locations (Bastille-Rousseau et al., 2020), and all locations were classified as day (6am to 6pm) or night and wet or dry season using dummy coding. All environmental covariates, described above, were extracted for each used and available location. Finally, individual-year-season datasets with less than 500 observed relocations or with no observed relocations in crops were removed.

We used exponential mixed-effects RSFs estimated using a logistic regression to evaluate resource selection. Model selection by AICc was performed using a population-level RSF with a random effect for individual (Bastille-Rousseau et al., 2020), and the most parsimonious model was then fit to each individual-year-season. Coefficient values and 95% confidence intervals were obtained for each individual-year-season model. To determine performance of the individual models, k-fold cross validation using 5 folds was performed for each model.

Drivers of similarity in resource selection

To address our first objective to determine how crop use affects overall resource selection strategies, we applied unsupervised random forest models with 10,000 trees to the RSF coefficients from each individual-year-season model. The random forest produces a proximity matrix that represents a measure of similarity between each individual-year-season. This proximity measure indicates how frequently a pair of individual-year-seasons were classified in the same terminal node of a tree by the random forest algorithm, with values ranging from 0 to 1 where 1 indicates perfect similarity. We then assessed the influence of environmental, seasonal, annual, and individual factors on similarity. We used a beta regression of the proximity metric and weighted the regression by the product of the k-fold cross validation scores for the associated pair of RSF models. Covariates included sex (coded as different sex, both male, or both female), season (different season, both wet, both dry), year (different year, same year), region (different region, both Serengeti, both Mara), difference in crop use defined as the difference in percentage of observed relocations spent in crops for the associated year-seasons, and difference in protected area use defined as the difference in percentage of observed relocations spent in protected and unprotected areas. We developed six hypotheses that informed our inclusion of specific variables and interactions and fit a single global model to test these. The hypotheses and expected effects are shown in Table 7.

Spatially Explicit Crop Selection

To investigate our second objective to understand how crop selection varies in relation to protected areas and agricultural composition, we divided the study system into two regions of hard-edge high fragmentation (Serengeti) and soft-edge low fragmentation (Masai Mara) following our assessment of landscape fragmentation metrics. To account for space, we stratified the unprotected area of both regions into 1000m non-overlapping buffers corresponding to the distance from protected areas. We used 1000m buffers extending to 3km, and a final buffer level encompassing elephant range from 3-6km from protected areas. Based on previous conflict assessments, relocations further than 6km were assumed to be related to dispersal events rather than crop raiding and were discarded (Tiller, 2017). Constant buffers of 250m corresponding to mean hourly step length were also tested and produced a similar spatial pattern indicating model results were not sensitive to buffer size, but we chose to use 1000m buffers for clear interpretation. All elephant relocations were assigned a region and buffer level, which was coded as a multi-level factor. We fit separate region-season RSFs using generalized linear regressions with a logit link. We used crop and buffer level as the two covariates and included an interaction between them to assess how crop selection changed in relation to buffer level. Because not all elephants used all buffer levels, we pooled individuals by region and year. Coefficients and 95% confidence intervals were extracted for each model. To assess goodness-of-fit, Area Under Curve values were calculated for each model, and we chose 0.7 as a cutoff value for reasonable model fit (Lemeshow and Hosmer, 1982).

To help interpret our findings, we calculated several landscape metrics within each regional buffer that could test for differences in the availability of crops and forest (percentage of total land area), and the size and shape of farm and forest patches (mean patch area, mean core area, and perimeter-area ratio) (Wang et al., 2014). We chose to focus on forest due to previous findings that forest patches play a key role as a cover habitat in facilitating crop use (Sitati and Walpole, 2005; Tiller, 2017). All metrics were calculated using the landscapemetrics package in R (Hesselbarth et al., 2019).

3. Results

After excluding individual-year-season datasets with no observed relocations in crops or with fewer than 500 total relocations in the dataset, 181 elephant-years from 56 individuals were included in the analyses. There were 176 elephant-year-seasons during the dry season and 157 during the wet season.

Individual Variation in Selection

We found wide variation in individual selection coefficients. The global model including all covariates and an interaction between crops and time of day was the most parsimonious model and was used to fit individual RSFs. However, while the coefficient confidence intervals for the population-level RSF did not overlap zero, individual coefficient estimates ranged from negative to positive for most covariates (Fig. 12). While only 21 (6.2%) individual-year-seasons showed selection for crops with confidence intervals that did not overlap zero, 184 (55.1%) showed selection for crops at night. Most individuals showed avoidance or no selection for higher settlement densities, while individuals varied greatly in selection for distance to primary and secondary roads and to protected areas. There was generally strong selection for forest/thicket and avoidance of grassland/savannah and slope, while selection for open woodland/bushland and NDVI covariance varied much more (Fig. 12). Summarized results for the individual-year-season models can be found in Figure 12.

Drivers of proximity in selection strategies

Proximity analyses indicated similarity between individual elephant-year-seasons was weak, with a mean proximity index value of 0.03 (min = 0.005, max = 0.7), demonstrating that elephant selection strategies varied by year. In support of our hypothesis that crop use is a key driver of resource selection strategies, the beta regression model indicated that similarities in overall selection strategies were driven by the degree of crop use in the dry season, as well as similar space use, similar sex, and similar seasons (Table 8). However, being in the same year had no effect (Table 8). Covariates related to space use and season appeared to be the most consistent driver of similarity in selection strategies. In contrast, we found that closer levels of crop use had a strong effect on similarity in the dry season, but not in the wet season (Table 8). Overall, we found repeatability in an individual's selection strategies between years, but accounting for season showed that this repeatability occurred mainly during the dry season, and there was no similarity in the wet season (Table 8).

Crop Selection in Space

In our assessment of landscape patch characteristics for crops and forest, we found that the Mara and Serengeti regions differed substantially. The Mara was characterized by approximately 5 times less crop cover and 2.5 times higher amounts of forest across all buffers (Fig. 13d). Compared to the Serengeti, crop patch area in the Mara were approximately 3.5 times smaller (Fig. 13a,b) and slightly more complex (Fig. 13c), while forest patches were 2.5 times larger and slightly less complex.

Relatedly, we detected differences in the spatial pattern of selection for crops between the two regions. Here we focus on the dry season, but wet season model results are also presented (Fig. 14, Table B3). In the Mara, selection for crops during the dry season occurred in the 1000m buffer ($\beta = 0.198$; 95% CI[0.182,0.213]) and was strongest in the 2000m buffer ($\beta = 0.535$; 95% CI[0.451,0.619]), while there was no selection for crops in the 3000m buffer ($\beta = 0.051$; 95% CI[-0.045,0.148]) (Fig. 14a). This pattern of selection appeared to be the inverse of selection for the buffered area in general, with the 2000m buffer being avoided most strongly ($\beta = -0.283$, 95% CI[-0.303, -0.264]), but experiencing the strongest selection for crops. In contrast, elephants in the Serengeti during the dry season selected most strongly for crops in the 1000m buffer ($\beta = 0.597$; 95% CI[0.547, 0.646]), and this diminished linearly for the 2000m ($\beta = 0.355$, 95% CI[0.299, 0.412]) and 3000m buffers ($\beta = 0.202$, 95% CI[0.139,0.265]) (Fig 14c). The selection for the buffered area followed the same pattern, with the 1000m buffer being selected most strongly ($\beta = 1.181$, 95% CI[1.157, 1.204]) and diminishing linearly. Notably, in both regions, selection for crops across the entire unprotected area was negative in the dry season. Dry season models (Mara AUC = 0.72, Serengeti AUC = 0.76) had reasonable goodness-of-fit, but this was not the case for wet season models (Mara AUC = 0.59, Serengeti AUC = 0.61). Coefficient estimates and 95% confidence intervals for all models can be found in Table B3.

4. Discussion

Understanding how spatially-explicit behaviors shape space use and resource requirements is of increasing interest. However, variation within a population can make this difficult to quantify. Using GPS tracking data from African elephants across two regions with markedly different wildland-agricultural interfaces, we developed approaches to quantify how crop use impacts resource selection strategies and crop selection changes in relation to landscape fragmentation and protected areas. Our results highlighted how crops, season, and space use play an important role in driving resource selection strategies, and how fragmentation affects where elephants prefer to use crops.

We found high individual variation in resource selection but identified several key trends that appeared to shape selection strategies. Space use and sex appeared to be the most consistent driver of similarity, while crops had a strong effect only in the dry season. Intra-individual similarity between years was also much closer in the dry season, while elephants appeared to have different selection strategies in the wet season from year to year. The dry season is also when crop use by elephants is highest in this system and the differences in crop use between individuals are most stark (i.e., those that raid crops and those that do not). This suggest that crops play an important role in shaping seasonal resource selection strategies in the system. Additionally, elephants that spent similar time in unprotected areas were more likely to have similar resource selection coefficients. Previous findings have shown that elephants change their behavior to use crops, including shifting their ranges as crops mature (Branco et al., 2019), changing daily activity budgets (Hahn et al., 2021), and altering their movement patterns prior to raiding (Troup et al., 2020). Our results suggest these behaviors require elephants to adjust their overall foraging strategy during periods of crop use in a relatively similar way. The similarity in selection strategies may also lead to more intraspecific competition among elephants that use crops in the dry season.

We also found strong spatial structuring in crop selection based on distance from protected areas, the extent of fragmentation, and the patch structure of crops and forest. Notably, when not accounting for spatial structure we found that elephants strongly avoided crops, but adding spatial structure to the model revealed zones that elephants selected and avoided for. With more fragmentation and smaller forest patches to use in the Serengeti, elephants selected strongly for crops close to the protected area boundary. In the Mara, we found a strong signal for selection in the 2000m buffer despite no large differences in the amount of crops or forest compared to other buffers. This is likely due to the spatial distribution of conflict hotspots in the Mara system within this buffer, and similar results were previously observed in a spatial conflict assessment of a subregion of the Mara (Tiller et al., 2021). While this signal may be unique to the Mara, it indicates that a softer edge between natural and cultivated land can allow elephants to move further into unprotected areas and in turn shift conflict risk to farms. The importance of forest patches to this movement behavior aligns with previous work showing that elephants and other species rely on extant forest to access crops and limit detection from humans (Hahn et al., In Review.; Tiller, 2017). Overall, our results suggest that the landscape structure and the ability of animals to move through it plays an important role in determining where conflict may occur and points to how conflict risk may change as land around protected areas are converted.

Several caveats to our approach should be noted. First, while we detected several factors that drove similarity between individuals, proximity between individuals was very low overall. Second, our ability to compare spatially structured crop selection in the Mara and Serengeti is only correlative due to the observational nature of this study. Third, while the low predictive power of the agricultural buffer models was typical for elephants where individual variation is high, it limits the extension of these findings beyond the study system. Based on our results, a controlled study or one using simulated landscapes (e.g. Signer et al., 2017) may be valuable to further explore how variation in animal response to fragmentation, forest cover, and protected areas can impact population distributions. This could prove useful for limiting human-wildlife conflict through landscape planning exercises such as wildlife dispersal areas and corridors (Buchholtz et al., 2020).

Quantifying variation between individuals can help identify key properties structuring population heterogeneity and the drivers of population distribution patterns (Bastille-Rousseau et al., 2019; Spiegel et al., 2017). Relating this variation to spatially explicit behaviors such as crop use can provide further context on the impact of differing behavioral responses to human development and landscape change. Given the increasing interest in the role of intra- and inter-individual variation in population dynamics, our findings represent an important step towards understanding how this variation shapes wildlife responses to accelerating land development from humans. While our study focused on elephant crop use, our approach is translatable to other species that are prone to conflict or adversely affected by human agricultural development. This may be most productive for species where variation in conflict risk between individuals has already been documented, such as carnivore depredation of livestock and bears accessing human food resources. Such investigations can play an important role in informing mitigation efforts and land use planning initiatives that incorporate behavioral complexity in human–wildlife conflict hotspots.

5. Tables & Figures

Table 7. Hypotheses were developed for each set of covariates to help determine the drivers of proximity in resource selection strategies among elephants. Region refers to the Mara and Serengeti regions. Land use was defined as protected and unprotected. All percentages are defined as the difference in percent of relocations between a pair of individual-year-seasons.

Hypothesis	Covariates	Expected Effect
Same individual and season (different years) drives proximity	Individual*Season	+
Similar agricultural use drives proximity in the dry season	% Ag*Season	-
Similar space use drives proximity	Region + % Protected + % Unprotected	+ Region / - % Land use
Same sex drives proximity	Sex	+
Same season or year drives proximity	Season + Year	+

Table 8. Model results showing drivers of proximity between elephants based on resource selection coefficients. Bold lines indicate where 95% confidence levels do not overlap zero. Hypothesis details can be found in Table 1. Reference levels for all factors were set as 'different', e.g. 'different sex' between a pair of individual-year-seasons. Crop use in the dry season was the strongest driver of similarity between different individuals, while within-individual repeatability between years was strong but only in the dry season.

Hypothesis	Term	Estimate	Std Error	Lwr.95	Upr.95
	(Intercept)	-3.558	0.015	-3.587	-3.529
Repeatability	**subject [same]**	**0.364**	**0.033**	**0.3**	**0.429**
	season [dry]:subject_name[same]	**0.772**	**0.047**	**0.68**	**0.864**
	season [wet]:subject_name [same]	0.079	0.059	-0.036	0.195
Crop use	pct.crop	-0.008	0.129	-0.261	0.244
	season [dry]:pct.crop	**-0.619**	**0.239**	**-1.087**	**-0.152**
	season [wet]:pct.crop	0.138	0.193	-0.24	0.516
Space use	**region [masai mara]**	**0.114**	**0.012**	**0.091**	**0.137**
	region [serengeti]	**0.091**	**0.012**	**0.068**	**0.115**
	pct unprotected	**-0.139**	**0.019**	**-0.176**	**-0.103**
	pct protected	**-0.078**	**0.016**	**-0.12**	**-0.047**
Sex	**sex [female]**	**0.074**	**0.011**	**0.052**	**0.096**
	sex [male]	**0.082**	**0.011**	**0.06**	**0.104**
Season & Year	**season [dry]**	**0.074**	**0.014**	**0.046**	**0.102**
	season [wet]	**0.063**	**0.014**	**0.036**	**0.091**
	year [same]	0.012	0.012	-0.011	0.035

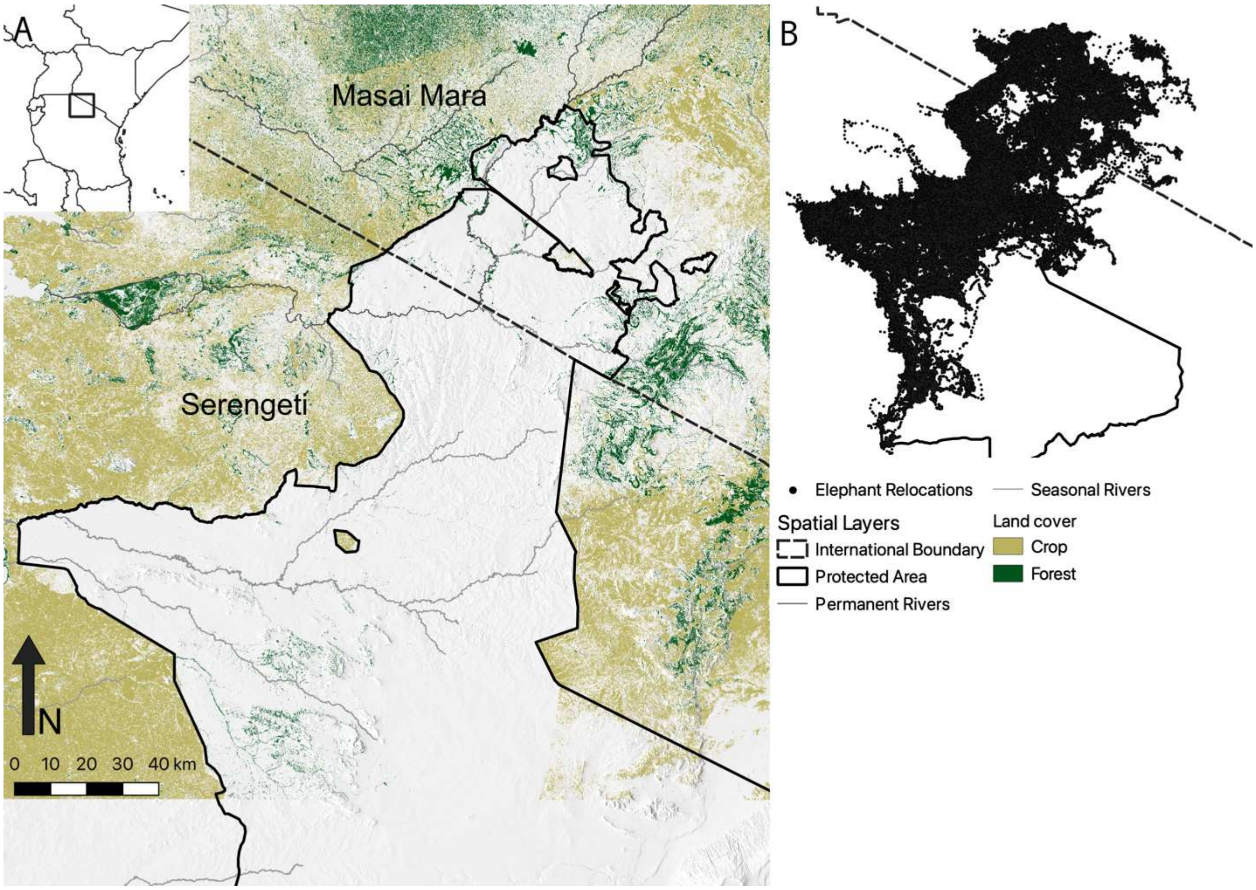

Figure 11. A) The Greater Serengeti-Mara Ecosystem showing protected areas, key land cover classes (crops and forest), permanent and seasonal rivers, and topography. Protected area boundaries have been simplified. B) Shows the GPS relocations of the 56 individuals included in the study.

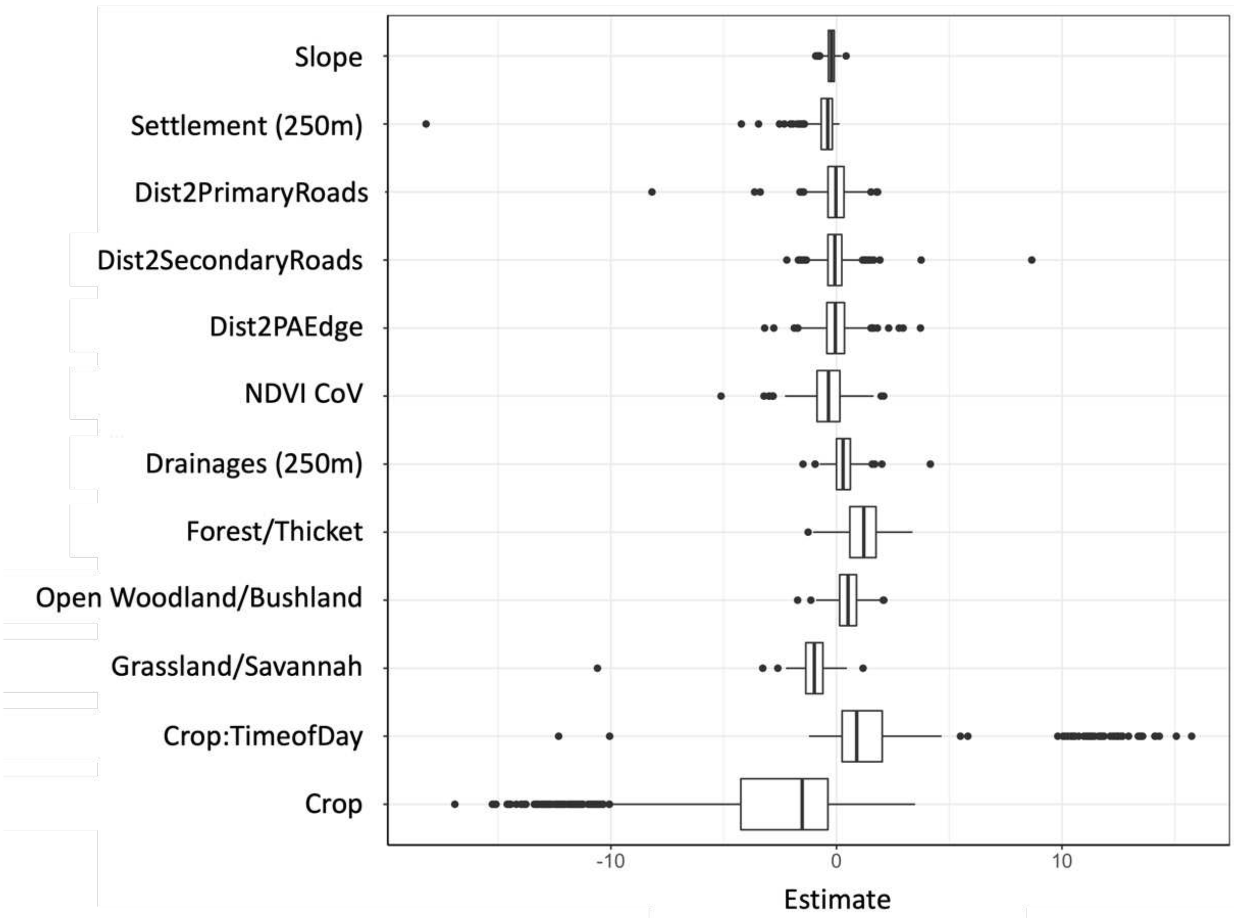

Figure 12. Results of 186 individual-year-season RSF models are summarized using boxplots to show the distribution of coefficient estimate for each covariate. An estimate of 0 indicates no selection, while positive estimates indicate selection and negative estimates indicate avoidance.

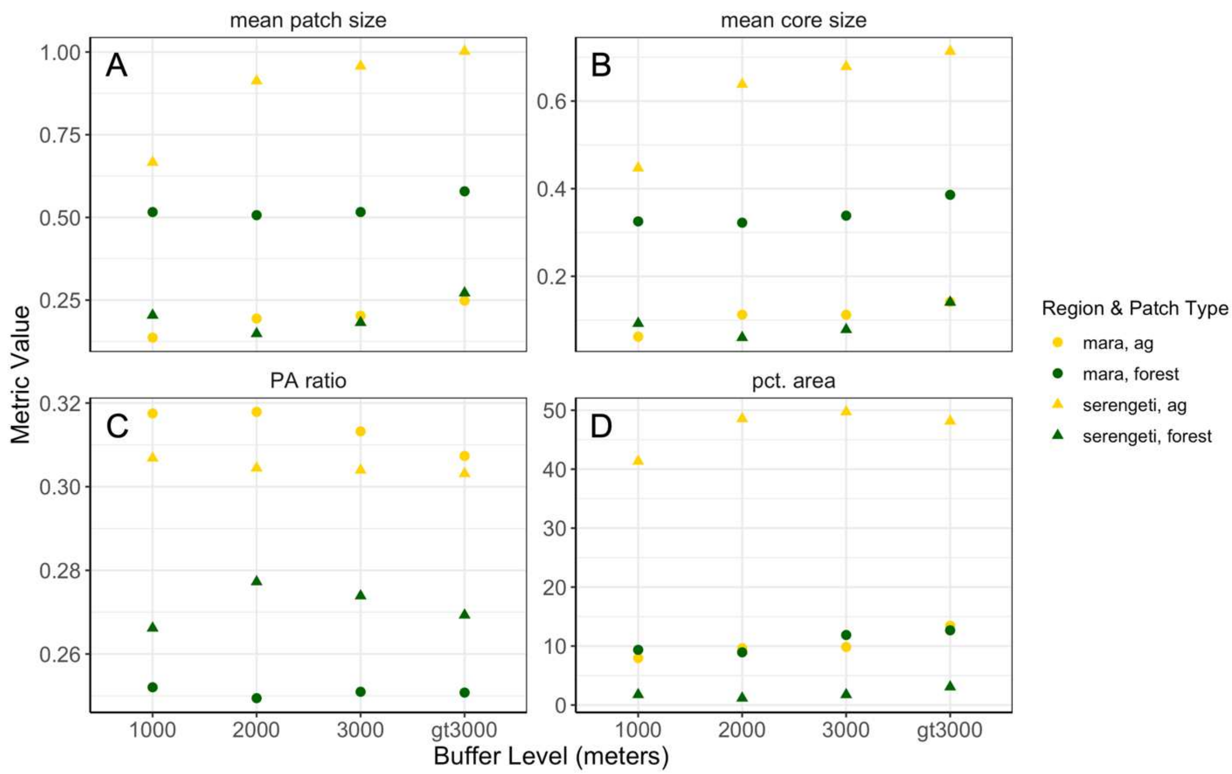

Figure 13. Landscape metrics highlight the strong differences in the wildland-agricultural interface measured as mean patch size (Ha), mean core patch size (Ha), perimeter-area ratio, and the percent area covered by crops and forest for each buffer level outside the Mara and Serengeti protected areas. Colors correspond to patch type (yellow = crops and green = forest) and shape corresponds to region (circles = Masai Mara and triangles = Serengeti).

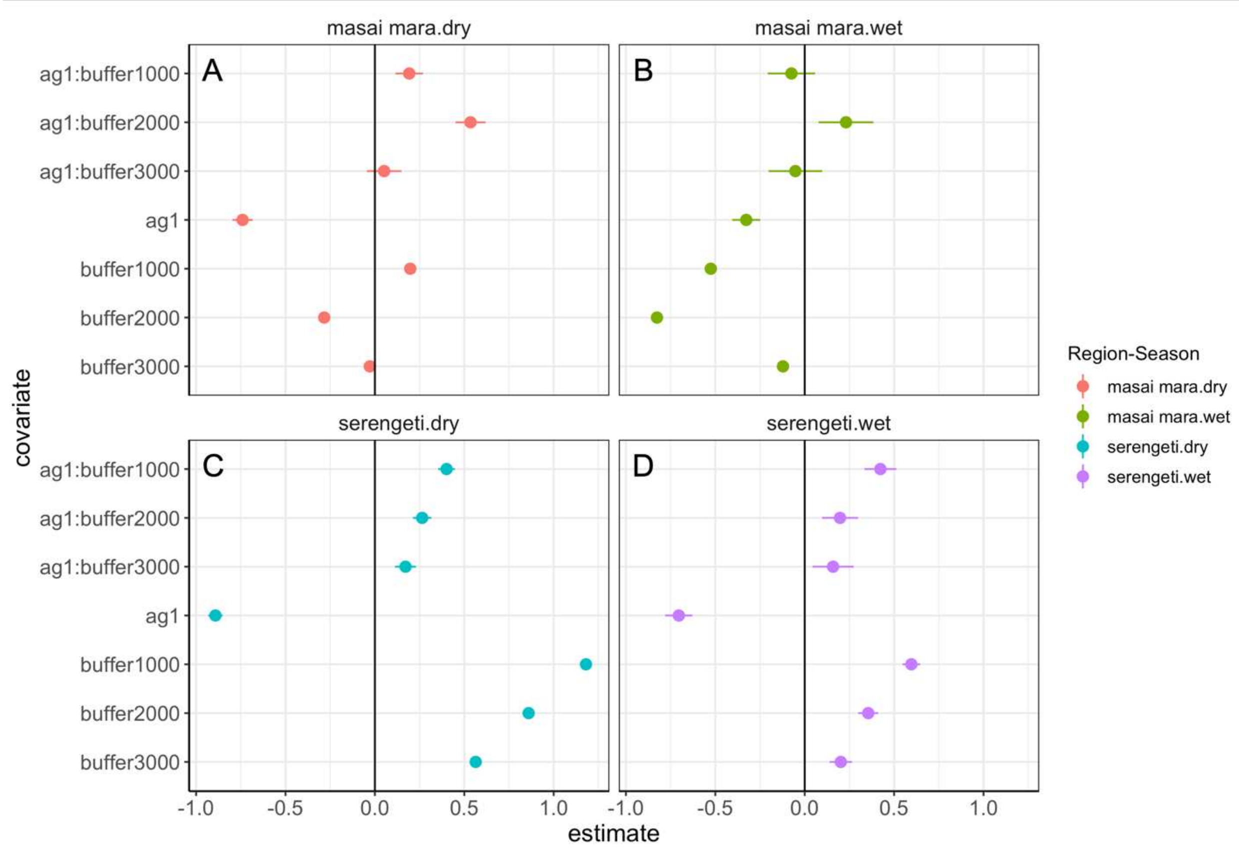

Figure 14. Selection of crops in relation to buffer levels outside protected areas are shown by region and season. Buffer levels of 1000, 2000, 3000, and >3000m were used, with the >3000m buffer used as the reference level. Bars represent 95% confidence intervals. Selection for crops without considering spatial context shows strong avoidance overall. However when accounting for spatial structure, the mara region shows a peak in selection for crops in the 2000m buffer, whereas selection in the Serengeti peaks at 1000m and tapers linearly.

6. References

Bastille-Rousseau, G., Wall, J., Douglas-Hamilton, I., Lesowapir, B., Loloju, B., Mwangi, N., Wittemyer, G., 2020. Landscape-scale habitat response of African elephants shows strong selection for foraging opportunities in a human dominated ecosystem. Ecography (Cop.). 43, 149–160. https://doi.org/10.1111/ecog.04240

Bastille-Rousseau, G., Wittemyer, G., Bastille-Rousseau, G., Wittemyer, G., 2019. Leveraging multidimensional heterogeneity in resource selection to define movement tactics of animals. Ecol. Lett. 22, 1417–1427. https://doi.org/10.1111/ele.13327

Blackwell, B.F., DeVault, T.L., Fernández-Juricic, E., Gese, E.M., Gilbert-Norton, L., Breck, S.W., 2016. No single solution: application of behavioural principles in mitigating human–wildlife conflict. Anim. Behav. 120, 245–254. https://doi.org/10.1016/j.anbehav.2016.07.013

Boyce, M.S., Vernier, P.R., Nielsen, S.E., Schmiegelow, F.K.A., 2002. Evaluating resource selection functions. Ecol. Modell. 157, 281–300. https://doi.org/10.1016/S0304-3800(02)00200-4

Branco, P.S., Merkle, J.A., Pringle, R.M., Pansu, J., Potter, A.B., Reynolds, A., Stalmans, M., Long, R.A., 2019. Determinants of elephant foraging behaviour in a coupled human-natural system: Is

brown the new green? J. Anim. Ecol. https://doi.org/10.1111/1365-2656.12971
Broekhuis, F., Madsen, E.K., Klaassen, B., 2019. Predators and pastoralists: how anthropogenic pressures inside wildlife areas influence carnivore space use and movement behaviour. Anim. Conserv. 1–13. https://doi.org/10.1111/acv.12483
Buchholtz, E.K., Stronza, A., Songhurst, A., McCulloch, G., Fitzgerald, L.A., 2020. Using landscape connectivity to predict human-wildlife conflict. Biol. Conserv. 248, 108677. https://doi.org/10.1016/j.biocon.2020.108677
Denninger-Snyder, K., Mneney, P., Benjamin, B., Mkilindi, P., Mbise, N., 2019. Seasonal and spatial vulnerability to agricultural damage by elephants in the western Serengeti, Tanzania. Oryx 1–11. https://doi.org/10.1017/S0030605318001382
Doherty, T.S., Driscoll, D.A., 2018. Coupling movement and landscape ecology for animal conservation in production landscapes. Proc. R. Soc. B Biol. Sci. 285. https://doi.org/10.1098/rspb.2017.2272
Farr, T.G., Rosen, P.A., Caro, E., Crippen, R., Duren, R., Hensley, S., Kobrick, M., Paller, M., Rodriguez, E., Roth, L., Seal, D., Shaffer, S., Shimada, J., Umland, J., Werner, M., Oskin, M., Burbank, D., Alsdorf, D.E., 2007. The shuttle radar topography mission. Rev. Geophys. https://doi.org/10.1029/2005RG000183
Gaynor, K.M., Brown, J.S., Middleton, A.D., Power, M.E., Brashares, J.S., 2019. Landscapes of Fear: Spatial Patterns of Risk Perception and Response. Trends Ecol. Evol. 34, 355–368. https://doi.org/10.1016/j.tree.2019.01.004
Grill, G., Lehner, B., Thieme, M., Geenen, B., Tickner, D., Antonelli, F., Babu, S., Borrelli, P., Cheng, L., Crochetiere, H., Ehalt Macedo, H., Filgueiras, R., Goichot, M., Higgins, J., Hogan, Z., Lip, B., McClain, M.E., Meng, J., Mulligan, M., et al., 2019. Mapping the world's free-flowing rivers. Nature 569, 215–221. https://doi.org/10.1038/s41586-019-1111-9
Hahn, N.R., Wall, J., Denninger-Snyder, K., Goss, M., Sairowua, W., Mbise, N., Estes, A.B., Ndambuki, S., Mjingo, E.E., Douglas-Hamiliton, I., Wittemyer, G., 2021. Risk perception and tolerance shape variation in agricultural use for a transboundary elephant population. J. Anim. Ecol. 91, 112–123. https://doi.org/10.1111/1365-2656.13605
Hahn, N.R., Wall, J., Dininger-Snyder, K., Sairowua, W., Goss, M., Ndambuku, S., Eblate, E.M., Mbise, N., Kiambi, S., Wittemyer, G., n.d. Staging Behaviors Identify Spatial and Temporal Risk of Human-Wildlife Conflict. J. Appl. Ecol.
Hesselbarth, M.H.K., Sciaini, M., With, K.A., Wiegand, K., Nowosad, J., 2019. landscapemetrics: an open-source R tool to calculate landscape metrics. Ecography (Cop.). 42, 1648–1657. https://doi.org/10.1111/ecog.04617
Johnson, H.E., Breck, S.W., Baruch-Mordo, S., Lewis, D.L., Lackey, C.W., Wilson, K.R., Broderick, J., Mao, J.S., Beckmann, J.P., 2015. Shifting perceptions of risk and reward: Dynamic selection for human development by black bears in the western United States. Biol. Conserv. 187, 164–172. https://doi.org/10.1016/j.biocon.2015.04.014
Joly, P., 2019. Behavior in a changing landscape: Using movement ecology to inform the conservation of pond-breeding amphibians. Front. Ecol. Evol. 7, 1–17. https://doi.org/10.3389/fevo.2019.155
Leclerc, M., Vander Wal, E., Zedrosser, A., Swenson, J.E., Kindberg, J., Pelletier, F., Vander, E., Zedrosser, A., Swenson, J.E., Kindberg, J., Pelletier, F., 2016. Quantifying consistent individual differences in habitat selection. Oecologia 180, 697–705. https://doi.org/10.1007/s00442-015-3500-6
Lewis, D.L., Baruch-Mordo, S., Wilson, K.R., Breck, S.W., Mao, J.S., Broderick, J., 2015. Foraging ecology of black bears in urban environments: Guidance for human-bear conflict mitigation. Ecosphere 6, 1–18. https://doi.org/10.1890/ES15-00137.1
Lima, S.L., Zollner, P.A., 1996. Towards a behavioral ecology of ecological landscapes. Trends Ecol. Evol. 11, 131–135. https://doi.org/10.1016/0169-5347(96)81094-9
Mukeka, J.M., Ogutu, J.O., Kanga, E., Røskaft, E., 2019. Human-wildlife conflicts and their correlates in Narok County, Kenya. Glob. Ecol. Conserv. 18, e00620. https://doi.org/10.1016/j.gecco.2019.e00620

Mumby, H.S., Plotnik, J.M., 2018. Taking the Elephants' Perspective: Remembering Elephant Behavior, Cognition and Ecology in Human-Elephant Conflict Mitigation. Front. Ecol. Evol. 6, 122. https://doi.org/10.3389/fevo.2018.00122

Northrup, J.M., Hooten, M.B., Anderson, C.R., Wittemyer, G., 2013. Practical guidance on characterizing availability in resource selection functions under a use-availability design. Ecology 94, 1456–1463. https://doi.org/10.1890/12-1688.1

Paton, D.G., Ciuti, S., Quinn, M., Boyce, M.S., 2017. Hunting exacerbates the response to human disturbance in large herbivores while migrating through a road network. Ecosphere 8. https://doi.org/10.1002/ecs2.1841

Pittiglio, C., Skidmore, A.K., Van Gils, H.A.M.J., McCall, M.K., Prins, H.H.T., 2014. Smallholder farms as stepping stone corridors for crop-raiding elephant in northern Tanzania: Integration of Bayesian expert system and network simulator. Ambio 43, 149–161. https://doi.org/10.1007/s13280-013-0437-z

Pozo, R.A., Cusack, J.J., McCulloch, G., Stronza, A., Songhurst, A., Coulson, T., 2018. Elephant space-use is not a good predictor of crop-damage. Biol. Conserv. 228, 241–251. https://doi.org/10.1016/J.BIOCON.2018.10.031

Ricketts, Ricketts, T.H., Ricketts, Ricketts, T.H., Ricketts, 2017. The Matrix Matters: Effective Isolation in Fragmented Landscapes. Am. Nat. 158, 87–99. https://doi.org/10.2307/3078900

Robertson, B.A., Rehage, J.S., Sih, A., 2013. Ecological novelty and the emergence of evolutionary traps. Trends Ecol. Evol. 28, 552–560. https://doi.org/10.1016/j.tree.2013.04.004

Sawyer, H., Nielson, R.M., Lindzey, F., McDonald, L.L., 2006. Winter Habitat Selection of Mule Deer Before and During Development of a Natural Gas Field. J. Wildl. Manage. https://doi.org/10.2193/0022-541X(2006)70

Shaffer, L.J., Khadka, K.K., Van Den Hoek, J., Naithani, K.J., 2019. Human-Elephant Conflict: A Review of Current Management Strategies and Future Directions. Front. Ecol. Evol. 6, 235. https://doi.org/10.3389/fevo.2018.00235

Signer, J., Fieberg, J., Avgar, T., 2017. Estimating utilization distributions from fitted step-selection functions. Ecosphere 8. https://doi.org/10.1002/ecs2.1771

Sih, A., Ferrari, M.C.O., Harris, D.J., 2011. Evolution and behavioural responses to human-induced rapid environmental change. Evol. Appl. 4, 367–387. https://doi.org/10.1111/j.1752-4571.2010.00166.x

Simon, R.N., Fortin, D., 2019. Linking habitat use to mortality and population viability to disarm an ecological trap. Biol. Conserv. 236, 366–374. https://doi.org/10.1016/j.biocon.2019.05.001

Sirko, W., Kashubin, S., Ritter, M., Annkah, A., Bouchareb, Y.S.E., Dauphin, Y., Keysers, D., Neumann, M., Cisse, M., Quinn, J., 2021. Continental-Scale Building Detection from High Resolution Satellite Imagery 1–15.

Sitati, A.N.W., Walpole, M.J., 2005. Factors Affecting Susceptibility of Farms to Crop Raiding by African Elephants : Using a Predictive Model to Mitigate Conflict. J. Appl. Ecol. 42, 1175–1182. https://doi.org/10.1111/j.1365-2664.2005.01091.x

Songhurst, A., McCulloch, G., Coulson, T., 2016. Finding pathways to human-elephant coexistence: A risky business. ORYX 50, 713–720. https://doi.org/10.1017/S0030605315000344

Spiegel, O., Leu, S.T., Bull, C.M., Sih, A., 2017. What's your move? Movement as a link between personality and spatial dynamics in animal populations. Ecol. Lett. 20, 3–18. https://doi.org/10.1111/ele.12708

Sukumar, R., Gadgil, M., 1988. Male-female differences in foraging on crops by Asian elephants. Anim. Behav. 36, 1233–1235. https://doi.org/10.1016/S0003-3472(88)80084-8

Tiller, L.N., 2017. Understanding how land-use change in the Trans Mara District, Kenya is driving human-elephant conflict and elephant movement. Kent Acad. Repos. University of Kent.

Tiller, L.N., Humle, T., Amin, R., Deere, N.J., Lago, B.O., Leader-Williams, N., Sinoni, F.K., Sitati, N., Walpole, M., Smith, R.J., 2021. Changing seasonal, temporal and spatial crop-raiding trends over 15 years in a human-elephant conflict hotspot. Biol. Conserv. 254, 108941. https://doi.org/10.1016/j.biocon.2020.108941

Troup, G., Doran, B., Au, J., King, L.E., Douglas-Hamilton, I., Heinsohn, R., 2020. Movement tortuosity and speed reveal the trade-offs of crop raiding for African elephants. Anim. Behav. 168, 97–108. https://doi.org/10.1016/j.anbehav.2020.08.009

Tyrrell, P., Amoke, I., Betjes, K., Broekhuis, F., Buitenwerf, R., Carroll, S., Hahn, N., Haywood, D., Klaassen, B., Løvschal, M., Macdonald, D., Maiyo, K., Mbithi, H., Mwangi, N., Ochola, C., Odire, E., Ondrusek, V., Ratemo, J., Pope, F., et al., 2022. Landscape Dynamics (landDX) an open-access spatial-temporal database for the Kenya-Tanzania borderlands. Sci. Data 9, 1–9. https://doi.org/10.1038/s41597-021-01100-9

Veldhuis, M.P., Ritchie, M.E., Ogutu, J.O., Morrison, T.A., Beale, C.M., Estes, A.B., Mwakilema, W., Ojwang, G.O., Parr, C.L., Probert, J., Wargute, P.W., Grant Hopcraft, J.C., Olff, H., 2019. Cross-boundary human impacts compromise the Serengeti-Mara ecosystem. Science (80-.). 363, 1424–1428. https://doi.org/10.1126/science.aav0564

Wall, J., Hahn, N., Carroll, S., Ndambuki, S., Goss, M., Siarowua, W., Tiedeman, K., Kiambi, S., Douglas-Hamilton, I., Wittemyer, G., In Review. Resource Selection by African Elephants in the Greater Mara Ecosystem, Kenya. *Mov*. Ecol.

Wang, X., Blanchet, F.G., Koper, N., 2014. Measuring habitat fragmentation: An evaluation of landscape pattern metrics. Methods Ecol. Evol. 5, 634–646. https://doi.org/10.1111/2041-210X.12198

Wittemyer, G., Northrup, J.M., Bastille-Rousseau, G., 2019. Behavioural valuation of landscapes using movement data. Philos. Trans. R. Soc. B Biol. Sci. 374, 20180046. https://doi.org/10.1098/rstb.2018.0046

CHAPTER 4: IDENTIFYING CONSERVATION TECHNOLOGY NEEDS, BARRIERS, AND OPPORTUNITIES

Summary

Amid accelerating threats to species and ecosystems, technology advancements to monitor, protect, and conserve biodiversity have taken on increased importance. While most innovations stem from adaptation of off-the-shelf devices, these tools can fail to meet the specialized needs of conservation and research or lack the support to scale beyond a single site. Despite calls from the conservation community of its importance, a shift to bottom-up innovation driven by conservation professionals remains limited. We surveyed practitioners, academic researchers, and technologists to understand the factors contributing to or inhibiting engagement in the collaborative process of technology development and adoption for field use, as well as identify emerging technology needs. High cost was the main barrier to technology use across occupations, while development of new technologies faced barriers of cost and partner communication. Automated processing of data streams was the largest emerging need, and respondents focused mainly on applications for individual-level monitoring and automated image processing. Cross-discipline collaborations and expanded funding networks that encourage cyclical development and continued technical support are needed to address current limitations and meet the growing need for conservation technologies.

1. Introduction

The integration of new technologies for conservation can improve how we monitor and measure changes to species and whole ecosystems (Marvin et al., 2016; Pimm et al., 2015; Wall et al., 2014), which is critical to guide and evaluate management and policy decisions (Snaddon et al., 2013). Technology can provide novel data sources, expanded spatial and temporal coverage, access to real-time information, and rapid processing and analysis for intervention (Pettorelli et al., 2014; Pimm et al., 2015; Ripperger et al., 2020; Xu et al., 2018). For example, the inclusion of real-time transmission and processing of data streams from acoustic devices has advanced remote detection and response to illegal logging (Liu et al., 2019). The rapid growth and availability of technologies has been driven largely by adapting existing and consumer-oriented technologies to fit specific conservation needs (Joppa, 2015), including hobby drones for monitoring and response to threats (Hahn et al., 2017; Koh and Wich, 2012) (Hahn et al., 2017; Koh & Wich, 2012), *in situ* molecular analyses in remote field settings (Pomerantz et al., 2018), radar data to forecast bird migrations at continental scales (Doren and Horton, 2018), and the application of blockchain protocols for fisheries supply chain management (Howson, 2020).

While these options are widely available for commercial application, they may lack features required for ecological conservation purposes such as limited durability and power efficiency, proprietary silos constraints, or high technical knowledge barriers (Gibb et al., 2019; Glover-Kapfer et al., 2019; Pearce, 2012a; Speaker et al., 2022). In other cases, adoption of data-rich and real-time sensors can lead to secondary problems with managing large datasets that often require their own custom approaches and pipelines (Doren and Horton, 2018; Norouzzadeh et al., 2018; Wall et al., 2014). Such constraints are thought to limit the uptake of new tools, but only recently have efforts been made to assess the degree to which they restrict the use of technologies in conservation settings and how to prioritize improvements for future development (Speaker et al., 2022).

In response to the limitations of off-the-shelf technologies, efforts have grown to actively create novel technologies geared towards conservation (Berger-Tal and Lahoz-Monfort, 2018; Pearce, 2012a). Conservation-driven efforts for purpose-built research and monitoring tools include hardware with a lower price compared with private consumer versions (Hill et al., 2018; Zárybnická et al., 2016), development of custom hardware to meet specific needs (Kalmár et al., 2019) and integration of existing platforms for real-time alerts (Weise et al., 2019). They may also require collaborations with technologists (defined as experts in technology-related fields including hardware engineering, software development, and machine learning) and companies to produce open-source products for research and management, such as Microsoft's MegaDetector (Beery et al., 2018), Google Earth Engine (Crego et al., 2021; Gorelick et al., 2017), Vulcan's EarthRanger (Vulcan, 2022), and Wildlife Insights (Ahumada et al., 2020). The bottom-up approach of small scale innovation puts increasing importance on cross-discipline collaborations between end users with first-hand knowledge of real world needs and existing obstacles (i.e., practitioners, researchers, and governments), and technologists, who have the skills to develop and adapt custom technologies (Berger-Tal and Lahoz-Monfort, 2018; Lahoz-Monfort et al., 2019).

A recent broad survey on the state of the conservation technology field identified that collaboration and information sharing across disciplines and projects was a primary opportunity (Speaker et al., 2022). For technology-based solutions to have substantial conservation impacts, there is a need for collaborations that effectively identify feature needs, share data, and facilitate iterative development and support (Joppa, 2015; Speaker et al., 2022). To facilitate development of conservation technologies and effectively leverage the support of technologists, we aimed to understand the factors contributing to or inhibiting engagement in the collaborative process of technology development and adoption for field use. We surveyed active conservation practitioners, researchers and conservation-oriented technologists regarding conservation technology development to answer three questions: 1) What are the technical barriers for technological uptake among end-users, and are development priorities focused on alleviating these?; 2) How are conservation technology collaborations structured, and what are the perceived barriers to successful collaborations?; and 3) To guide future development, what upcoming technologies are the conservation community looking for?

2. Results

Of the 101 completed survey responses, we categorized respondents into three groups: 53 were conservation practitioners, 42 were academic researchers, and seven were technologists. Familiarity and experience with conservation technologies varied widely among respondents. Most (71%) of respondents reported being extremely or very familiar with technologies, while 26% reported being moderately familiar. Most (96%) respondents also had experience using existing technologies for conservation applications, while fewer had experience in testing new or unproven tools (48%), adaptation or iterative development of existing tools (54%) or design of new tools (34%). Among user groups, more conservation practitioners were engaged in the development of new conservation technologies (71%) compared to academic researchers (45%).

To address our first question, the technical barriers for using technologies identified by conservation practitioners and academic researchers were similar, highlighting durability (OR = 2.48, 95% CI[1.44 – 4.26]), cost (OR = 8.91, 95% CI[5.07 – 15.65], power efficiency (OR = 4.24, 95% CI[2.45 – 7.35], data management (OR = 2.42, 95% CI[1.39 – 4.22]), and real-time transmission (OR = 3.59, 95% CI[2.03 – 6.35]), (Fig. 15a). However, only cost (OR = 6.10, 95% CI[3.02 – 13.16]) was identified as likely to prevent the use of a technology in the field (Fig. 15b). Development priorities that were highly ranked among practitioners and researchers were aligned with reported technical issues: durability (OR = 7.65, 95% CI[3.09 – 18.97]), cost (OR = 4.34. 95% CI[1.84 – 10.22], and power efficiency (OR = 3.74, 95% CI[1.57 – 8.88]) (Fig. 15c). In the limited responses from technologists, we found feature priorities were focused on cost (7/7 respondents included cost in the top three) and ease of use (4/7). In contrast, durability (2/7 in top three) and power efficiency (1/7) were not highly ranked among technologists (Fig D1).

For our second question, we recorded 84 unique collaborations ranging from 2 to 15 partners (median of five partners). Of the collaborations, 93% involved practitioners, 68% involved academic researchers, and 58% involved technologists. Only 29% of collaborations used websites or forum resources (e.g. wildlabs.net), but 75% of these occurred in a collaboration without a tech expert. Technologists were disproportionately involved in the design stage, while practitioners and researchers were mainly involved in the testing and use phase (Fig D2). Among barriers to collaborations with conservation technology, high cost (53%) was reported most frequently, followed by delayed timelines (41%) and lack of technical support (25%) (Fig. D3). In terms of factors affecting collaboration experience, our model with poor communication between conservationists and technologists (OR = 0.23, 95% CI[0.06-0.96] and high cost (OR = 0.34, 95% CI[0.11-1.02]) was the most parsimonious model in explaining poor collaborations (Table D1).

In response to our third question, we identified several strong themes for desired future technologies. Most of the listed technologies were improvements or extensions to existing tools (e.g. mesh network tracking tags, field-ready genetic analysis kits), while some had specific use cases, such as a device to non-invasively collect and protect hair samples for DNA analysis (Table D2). Automation was mentioned in nearly one third of responses (32/101), with most use cases for automation in reference to animal image processing (53%) and individual-level monitoring (22%) (Fig 16b). Additionally, researchers were largely focused on automation advancements, while practitioners listed a more diverse set of feature needs (Fig. 16a). For all responses on desired technologies, individual-level monitoring (51%) and animal image processing (28%) were the most-mentioned use cases.

3. Discussion

The shift in conservation technology from adaptation of off-the-shelf devices to bottom-up innovation requires a strong collaborative environment and solid understanding of the current and future needs of conservation practitioners and researchers (Berger-Tal and Lahoz-Monfort, 2018). Our assessment of technical barriers identified frequent issues with multiple feature types but cost disproportionately prevented the use of technologies in conservation and research settings. While previous studies have touted advanced technologies as a cost-effective pathway to expand the reach and resolution of environmental monitoring (Koh and Wich, 2012; Pimm et al., 2015), our results suggest that the high upfront cost of new technologies puts currently-available tools out of reach for many groups. These costs manifest across device purchase, training and implementation time, maintenance, data storage, and processing. In addition, low cost is often misaligned with other features that respondents identified, such as durable environment-proofing and robust technical support. For example, the popular AudioMoth low-cost acoustic monitoring platform is sold without a protective case for 60 USD, but users can purchase a case for 35 USD (AudioMoth, 2021). While this extra durability increases the cost by over 50%, the design demonstrates a flexible approach to keep prices low for users who do not require robust environmental protection or can build their own solution.

Our assessment of collaboration structures found that just over half involved a technologist, which may explain the highly reported issues with delayed timelines and lack of technical support. While lack of communication between partners was only reported in 17% of responses, it was the most significant contributor to poor collaborations. This appears to stem from identified issues that end users were under-represented in the development and adaptation stages of the development cycle, and technologists were under-represented in the testing and use phases. While reports of conservation technology failures are not widely reported in the literature, our results align with themes from successful technology applications. For example, the ElephantBook tool (Kulits et al., 2021) was developed between a team of computer scientists, students, researchers, and conservation managers to aid re-identification of elephants using machine learning. They improved functionality by integrating with existing data platforms and have continued to provide technical support to advance the tool (Kulits et al., 2021). Similarly, Snapshot Safari (Pardo et al., 2021) has found success with cyclical development in collaboration with multiple stakeholders and technologists. The project provides a platform for camera trap data processing and has slowly expanded to include more study sites, expanded functionality to allow tagging by citizen scientists, and added machine learning to pre-process images (Pardo et al., 2021).

Additionally, our limited data from technologists suggest a different set of feature priorities for conservation technologies, highlighting the importance of involving end-users from the beginning to ensure that tool specifications meet conservation needs (Lahoz-Monfort et al., 2019). Potential solutions to this include adopting a 'lean start-up' approach used in commercial sectors that seeks to identify end-users, define features prior to development, and iteratively improve on new products (Iacona et al., 2019). In concert, platforms like Wildlabs.org and events such as technology challenges and hackathons (e.g. conservationxlabs.com) can allow end users and developers to connect around conservation problems and foster cross-discipline collaborations. However, further research on the success and limitations of these avenues could help improve and expand networking options in the future. Further, documenting tools and operating instructions in white papers, publications, or setup and troubleshooting guides (e.g. AuidoMoth Getting Started Guide), could help uptake by end users. In the absence of direct technology support, websites and forums also appeared to be an important source of information among respondents. Conservation technology sites that collate solutions (e.g. Wildtech.mongabay.com) and platforms that facilitate networking and information sharing (e.g. Wildlabs.org) can be a viable solution to alleviate some of the technical knowledge roadblocks to the development and use of technologies in practice.

Our assessment of emerging needs in the conservation technology space identified software-based automation tools as the largest desire. Many respondents referenced the need to handle the increasing size of data streams, suggesting that automation is an important need among the conservation community. This aligns with recent results from a broad survey of the conservation technology field pointing to the need to enhance capacity for large-scale data analyses (Speaker et al., 2022). Surprisingly, many of the ideas for automation technology already exist in some form, such as automated identification and counting of individual animals in camera trap images (Tabak et al., 2018). This suggests that scaling new devices and software beyond the original project may prove difficult when most end users lack the technical know-how and infrastructure to adapt it to their specific use case. One example of this scenario is AI-based classification and detection models for camera trap images, where the drift in species assemblages and environments between sites can severely degrade classification performance (Beery et al., 2018), and where users require the skills or collaborators to implement models and code from open source repositories. Tools developed by Google's Wildlife Insights (Ahumada et al., 2020) are now available for researchers to process data for a wide range of species and habitats with a simple user interface. In other cases, automation improvements in one area may lead to secondary problems. For example, real-time tracking data of wildlife using accelerometer sensors can automatically flag immobility due to injury or poaching (Wall et al., 2014) but requires in-depth analysis of specificity and sensitivity to improve allocation of management resources (G. Wittemyer pers. comm. 2021).

To reduce existing barriers and meet the emerging needs of conservation professionals through bottom-up innovation, our results point to the importance of an adaptive development process that brings end-users to the table early and keeps developers involved beyond the initial release. In the commercial and industrial sectors, spiral development processes with build-test-feedback-revise iterations are shown to get products to market quicker (Cooper, 2014). Further, companies that focus on the voice of the customer can build better and longer-lasting products (Cooper, 2019). In the conservation sphere however, continual developer support may not always be feasible as pro-bono engineers switch to new projects or grant cycles end (Berger-Tal and Lahoz-Monfort, 2018). In these cases, establishing a strategy to build financially sustainable products using alternative funding models from the beginning of the project may help sustain the tool beyond the end of the initial funding cycle. Research on financial models for conservation technology are limited (Speaker et al., 2022), but opportunities include open-source designs that can be community-maintained (Pearce, 2012b), social impact enterprises that follow commercial strategies to maximize environmental impact alongside profits (Mair et al., 2012), or public-private partnerships that have been used to support technology growth in other underfunded sectors (Meissner, 2019). In concert, the funding network for conservation technologies can encourage best practices of iterative development and continued product support, while reducing cost barriers to scale beyond pilot sites. To achieve the full potential of conservation technologies through small-scale innovation, we must continue to foster collaborations across disciplines, sustain product support, and seek alternative funding models for future tech developments.

4. Methods

Survey

We identified our survey population using groups with a conservation or conservation-technology focus. First, we selected groups for which 1) there was active membership; 2) members were likely to have at least some familiarity with technology for conservation; and 3) it was possible to obtain the number of people that the survey was sent to estimate response rates. We also sought to distribute the survey to groups that would capture practitioners and scientists working in diverse fields and environments. We also identified groups that would have a high percentage of technology experts. Through this process we identified 11 groups: Society for Conservation Biology Working Groups for Freshwater, Conservation Technology, and Animal Behavior in Conservation, Snapshot Safari, Wildlife Insights, Vulcan EarthRanger developers, Smithsonian Institute, San Diego Zoo Wildlife Alliance, Wildlabs, and the AI for Conservation Slack channel. We dropped the Society for Conservation Biology Conservation Technology working group because we received no responses.

The survey instrument (Appendix D Survey Instrument) was distributed via email and listserv postings to each group. In the case of the AI for Conservation group, the survey was sent through Slack. Due to privacy requirements, it was not always possible to collect individual email addresses for distribution, so it was possible for a person to receive the survey multiple times if they were a part of different distribution groups. The survey consisted of 24 questions, involving a combination of multiple-choice, Likert-scale (Likert, 1932), and open-response questions. The survey was designed to answer three overarching research questions: 1) What are the technical barriers for technological uptake among end-users, and are development priorities focused on alleviating these?; 2) How are conservation technology collaborations structured, and what are the perceived barriers to successful collaborations?; and 3) What future technologies are the conservation community looking for?

To better-evaluate these questions, the survey was structured around two ways of interacting with conservation technology: 1) the use of technology tools for conservation and research, and 2) the development (i.e., design, adaptation, and testing) of new tools. Respondents were asked to specify their occupation from a list of 6 options. Due to the limited sample size, occupation was collapsed into three categories: conservation practitioners (front-lines conservationists, non-academia researchers and conservation facilitators), academic researchers (professor/faculty/postdoc and graduate student), and technologists. In conjunction, we defined four distinct roles that respondents could take on: Use of existing and established tools for work, testing of new or unproven tools, adaptation or iterative development of existing tools, and design of new tools. Respondents were allowed to select more than one role. We used skip logic to only show respondents questions relevant to their experience and roles with conservation technology.

We administered the survey online through Qualtrics from 10th July 2020 to 30th October 2020. To access the survey, respondents were required to consent to participate in our study and were assured that their responses would remain completely anonymous. The survey distribution list reached 648 people. Follow-up emails were sent to each group once, approximately one month after the initial email. We received 101 complete responses, for a response rate of 15.6%. Although this rate is relatively low (Mayer and Wellstead, 2018), it is consistent with other online surveys that used email to contact respondents (Archie et al., 2012; Jimenez et al., 2019). The survey was carried out according to the United States Federal Policy for the Protection of Human Subjects, and all protocols and methods were approved by Colorado State University's Institutional Review Board before implementation (Protocol No. 20-10050H). Informed consent was obtained from all participants.

Statistical Analysis

Descriptive statistics were reported as percentages. For all models, responses from technologists were withheld and evaluated separately due to low response rates from this occupation group. We conducted all statistical analyses using R version 4.0.3 and the ordinal package (Christensen, 2019; R Core Team, 2013).

To investigate our first question on technical barriers, we used two questions in the survey. First, to identify the prevalence of issues, we asked respondents to list the frequency at which they encountered different technical limitations. We used an ordinal logistic regression model to evaluate the frequency of occurrence, defined as Never to Always with five categories, in relation to technical limitation and occupation. We categorized seven possible limitations: 1. high or prohibitive cost; 2. lack of durability; 3. poor power efficiency; 4. data access limitations; 5. data management problems; 6. lack of interoperability with other devices or software; or 7. lack of or poor real-time data transmission. Durability was defined to respondents as features that prevented damage to tools (e.g. waterproofing, theft-proofing, etc.). Second, to determine the extent to which technical limitations impacted use of technologies, we asked respondents to indicate whether each limitation had prevented them from using a device or tool in the past. We used a logistic regression model to evaluate the prevention of use in relation to the technical limitation and occupation.

To investigate our question on conservation technology collaborations, we first quantified collaboration structures. For each collaboration, we calculated the percentage of collaborator types involved in each of the four roles (design, adapt, test, and use) of the development process. Collaborator types were collapsed into four categories: practitioners and non-academic researchers, academic researchers, technologists, and website and forum resources. To evaluate barriers, we first summarized the overall frequency of barrier types reported and evaluated the relationship between barriers and collaboration success using ordinal logistic regression models. We used Likert-scale (Likert, 1932) ratings of collaboration experience, defined as Poor to Excellent with five categories as the response variable ($n = 54$), and collaboration group size (continuous), type of technology (hardware or software), and collaboration limitations as possible predictors. Collaboration limitations were defined as: 1. high cost; 2. delayed timeline, 3. lack of project management, 4. misunderstanding on deliverables, 5. lack of technical support, 6. poor communication between conservationists and technologists, and 7. lack of partners. To select the most parsimonious model, we first fit a full model that included all covariates. From this full model, we sequentially dropped the least informative covariate (defined by minimum absolute value of b/SE) and refit the model. The higher order model was discarded if eliminating a covariate led to a reduction in AICc, and this approach was carried out until no additional covariate could be eliminated without leading to an increase in AICc (Arnold, 2010).

To investigate our question on emerging needs, we assessed unmet needs using answers derived from a theme analysis of the open-ended survey question "Assuming unlimited funding and resources, what technological solution would you want to see developed?". SB used NVivo 12 Pro ("Nvivo 12 Pro," 2020) to inductively (i.e., without predetermined categories) code responses into themes (Table D2, D3). After the initial coding, all authors re-examined, refined, and integrated codes, when necessary, based on our research objectives (Creswell and Creswell, 2017).

5. Figures

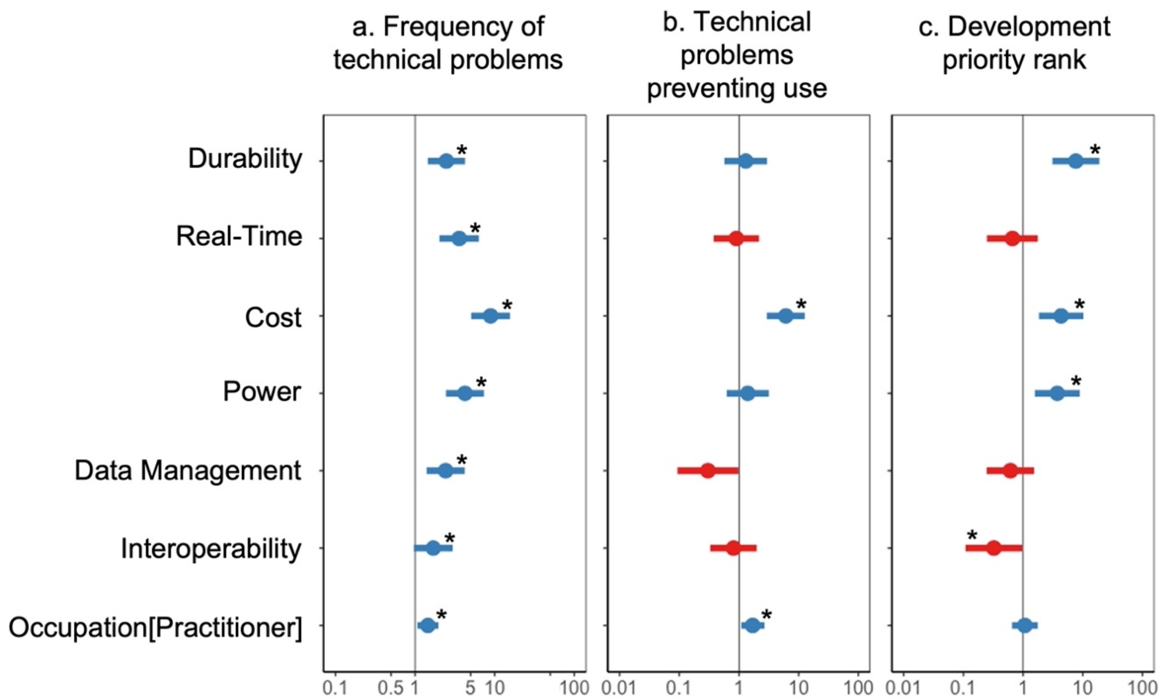

Figure 16. The importance of technology features as barriers to use and development priorities. Coefficient estimates (odds ratios) and 95% confidence intervals are shown for predicted relationships between feature types and a) the frequency of feature-related issues experienced during use, b) the frequency that feature-related issues prevented use of a tool or device, and c) the feature priority in development of new tools and devices. For A and B, blue circles indicate where respondents experienced more problems. For C, blue circles indicate where respondents ranked features with higher priority. Asterixis denote where coefficient estimates, and confidence intervals did not overlap 1 and indicate a significant influence.

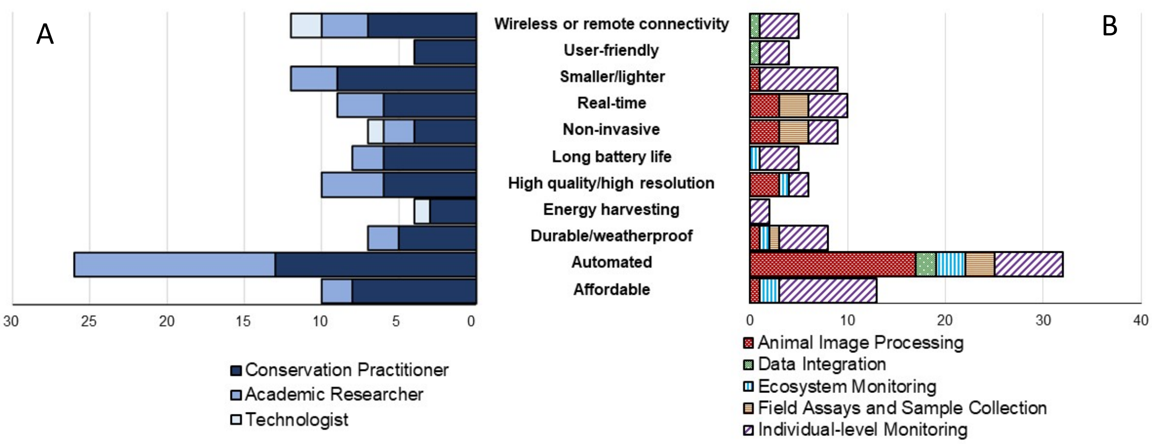

Figure 17. Categories of improvements to existing technology identified by occupation group and application type. The x-axis denotes the counts of respondents. Answers were derived from a theme analysis of the open-ended survey question "Assuming unlimited funding and resources, what technological solution would you want to see developed?". Theme analysis codebooks can be found in Table D2 and Table D3.

6. References

Ahumada, J.A., Fegraus, E., Birch, T., Flores, N., Kays, R., O'Brien, T.G., Palmer, J., Schuttler, S., Zhao, J.Y., Jetz, W., Kinnaird, M., Kulkarni, S., Lyet, A., Thau, D., Duong, M., Oliver, R., Dancer, A., 2020. Wildlife Insights: A Platform to Maximize the Potential of Camera Trap and Other Passive Sensor Wildlife Data for the Planet. Environ. Conserv. 47, 1–6. https://doi.org/10.1017/S0376892919000298

Archie, K.M., Dilling, L., Milford, J.B., Pampel, F.C., 2012. Climate change and western public lands: A Survey of U.S. Federal land managers on the status of adaptation efforts. Ecol. Soc. 17. https://doi.org/10.5751/ES-05187-170420

Arnold, T.W., 2010. Uninformative Parameters and Model Selection Using Akaike's Information Criterion. J. Wildl. Manage. 74, 1175–1178. https://doi.org/10.2193/2009-367

AudioMoth, 2021. AudioMoth [WWW Document]. Gr. Gets. URL https://groupgets.com/manufacturers/open-acoustic-devices/products/audiomoth

Beery, S., Van Horn, G., Perona, P., 2018. Recognition in Terra Incognita. Lect. Notes Comput. Sci. (including Subser. Lect. Notes Artif. Intell. Lect. Notes Bioinformatics) 11220 LNCS, 472–489. https://doi.org/10.1007/978-3-030-01270-0_28

Berger-Tal, O., Lahoz-Monfort, J.J., 2018. Conservation technology: The next generation. Conserv. Lett. 11, 1–6. https://doi.org/10.1111/conl.12458

Christensen, R., 2019. ordinal - Regression Models for Ordinal Data.

Cooper, R.G., 2019. The drivers of success in new-product development. Ind. Mark. Manag. 76, 36–47. https://doi.org/10.1016/j.indmarman.2018.07.005

Cooper, R.G., 2014. What's next? After stage-gate. Res. Technol. Manag. 57, 20–31. https://doi.org/10.5437/08956308X5606963

Crego, R.D., Masolele, M.M., Connette, G., Stabach, J.A., 2021. Enhancing Animal Movement Analyses : Spatiotemporal Matching of Animal Positions with Remotely Sensed Data Using Google Earth Engine and R.

Creswell, J.W., Creswell, D.J., 2017. Research design: Qualitative, quantitative, and mixed methods approaches. Sage publications.

Doren, B.M.V., Horton, K.G., 2018. A continental system for forecasting bird migration. Science (80-.). 361, 1115–1118. https://doi.org/10.1126/science.aat7526

Gibb, R., Browning, E., Glover-Kapfer, P., Jones, K.E., 2019. Emerging opportunities and challenges for passive acoustics in ecological assessment and monitoring. Methods Ecol. Evol. 10, 169–185. https://doi.org/10.1111/2041-210X.13101

Glover-Kapfer, P., Soto-Navarro, C.A., Wearn, O.R., 2019. Camera-trapping version 3.0: current constraints and future priorities for development. Remote Sens. Ecol. Conserv. 1–15. https://doi.org/10.1002/rse2.106

Gorelick, N., Hancher, M., Dixon, M., Ilyushchenko, S., Thau, D., Moore, R., 2017. Google Earth Engine: Planetary-scale geospatial analysis for everyone. Remote Sens. Environ. 202, 18–27. https://doi.org/10.1016/j.rse.2017.06.031

Hahn, N., Mwakatobe, A., Konuche, J., de Souza, N., Keyyu, J., Goss, M., Chang'a, A., Palminteri, S., Dinerstein, E., Olson, D., 2017. Unmanned aerial vehicles mitigate human–elephant conflict on the borders of Tanzanian Parks: a case study. Oryx 51, 513–516. https://doi.org/10.1017/S0030605316000946

Hill, A.P., Prince, P., Piña Covarrubias, E., Doncaster, C.P., Snaddon, J.L., Rogers, A., Prince, P., Piña, E., Patrick, C.C., Rogers, A., Hill, A.P., Piña Covarrubias, E., Doncaster, C.P., Snaddon, J.L., Rogers, A., 2018. AudioMoth: Evaluation of a smart open acoustic device for monitoring biodiversity and the environment. Methods Ecol. Evol. 9, 1199–1211. https://doi.org/10.1111/2041-210X.12955

Howson, P., 2020. Building trust and equity in marine conservation and fisheries supply chain management with blockchain. Mar. Policy 115, 103873. https://doi.org/10.1016/j.marpol.2020.103873

Iacona, G., Ramachandra, A., McGowan, J., Davies, A., Joppa, L., Koh, L.P., Fegraus, E., Game, E., Guillera-Arroita, G., Harcourt, R., Indraswari, K., Lahoz-Monfort, J.J., Oliver, J.L., Possingham, H.P., Ward, A., Watson, D.W., Watson, J.E.M., Wintle, B.A., Chadès, I., 2019. Identifying technology solutions to bring conservation into the innovation era. Front. Ecol. Environ. 17, 591–598. https://doi.org/10.1002/fee.2111

Jimenez, M.F., Laverty, T.M., Bombaci, S.P., Wilkins, K., Bennett, D.E., Pejchar, L., 2019. Underrepresented faculty play a disproportionate role in advancing diversity and inclusion. Nat. Ecol. Evol. 3, 1030–1033. https://doi.org/10.1038/s41559-019-0911-5

Joppa, L.N., 2015. Technology for nature conservation: An industry perspective. Ambio 44, 522–526. https://doi.org/10.1007/s13280-015-0702-4

Kalmár, G., Wittemyer, G., Völgyesi, P., Rasmussen, H.B., Maróti, M., Lédeczi, Á., 2019. Animal-Borne Anti-Poaching System, in: Proceedings of the 17th Annual International Conference on Mobile Systems, Applications, and Services. ACM, New York, NY, USA, pp. 91–102. https://doi.org/10.1145/3307334.3326080

Koh, L.P., Wich, S.A., 2012. Dawn of drone ecology: Low-cost autonomous aerial vehicles for conservation. Trop. Conserv. Sci. 5, 121–132. https://doi.org/10.1177/194008291200500202

Kulits, P., Wall, J., Bedetti, A., Henley, M., Beery, S., 2021. ElephantBook: A Semi-Automated Human-in-the-Loop System for Elephant Re-Identification 88–98. https://doi.org/10.1145/3460112.3471947

Lahoz-Monfort, J.J., Chadès, I., Davies, A., Fegraus, E., Game, E., Guillera-Arroita, G., Harcourt, R., Indraswari, K., McGowan, J., Oliver, J.L., Refisch, J., Rhodes, J., Roe, P., Rogers, A., Ward, A., Watson, D.M., Watson, J.E.M., Wintle, B.A., Joppa, L., 2019. A Call for International Leadership and Coordination to Realize the Potential of Conservation Technology. Bioscience 69, 823–832. https://doi.org/10.1093/biosci/biz090

Likert, R., 1932. A technique for the measurement of attitudes. Arch. Psychol. 22, 55.

Liu, H., Li, W., Lv, G., 2019. How nonrandom habitat loss affects nature reserve planning strategies. Ecol. Modell. 397, 39–46. https://doi.org/10.1016/j.ecolmodel.2018.12.014

Mair, J., Battilana, J., Cardenas, J., 2012. Organizing for Society: A Typology of Social Entrepreneuring Models. J. Bus. Ethics 111, 353–373. https://doi.org/10.1007/s10551-012-1414-3

Marvin, D.C., Koh, L.P., Lynam, A.J., Wich, S., Davies, A.B., Krishnamurthy, R., Stokes, E., Starkey, R., Asner, G.P., 2016. Integrating technologies for scalable ecology and conservation. Glob. Ecol. Conserv. 7, 262–275. https://doi.org/10.1016/j.gecco.2016.07.002

Mayer, A.L., Wellstead, A.M., 2018. Questionable survey methods generate a questionable list of recommended articles. Nat. Ecol. Evol. 2, 1336–1337. https://doi.org/10.1038/s41559-018-0637-9

Meissner, D., 2019. Public-Private Partnership Models for Science, Technology, and Innovation Cooperation. J. Knowl. Econ. 10, 1341–1361. https://doi.org/10.1007/s13132-015-0310-3

Norouzzadeh, M.S., Nguyen, A., Kosmala, M., Swanson, A., Palmer, M.S., Packer, C., Clune, J., 2018. Automatically identifying, counting, and describing wild animals in camera-trap images with deep learning. Proc. Natl. Acad. Sci. U. S. A. 115, E5716–E5725. https://doi.org/10.1073/pnas.1719367115

Nvivo 12 Pro, 2020.

Pardo, L.E., Bombaci, S., Huebner, S.E., Somers, M.J., Fritz, H., Downs, C., Guthmann, A., Hetem, R.S., Keith, M., le Roux, A., Mgqatsa, N., Packer, C., Palmer, M.S., Parker, D.M., Peel, M., Slotow, R., Maartin Strauss, W., Swanepoel, L., Tambling, C., et al., 2021. Snapshot Safari: A large-scale collaborative to monitor Africa's remarkable biodiversity. S. Afr. J. Sci. 117, 2–5. https://doi.org/10.17159/SAJS.2021/8134

Pearce, J.M., 2012a. Building research equipment with free, open-source hardware. Science (80-.). https://doi.org/10.1126/science.1228183

Pearce, J.M., 2012b. The case for open source appropriate technology. Environ. Dev. Sustain. 14, 425–431. https://doi.org/10.1007/s10668-012-9337-9

Pettorelli, N., Laurance, W.F., O'Brien, T.G., Wegmann, M., Nagendra, H., Turner, W., 2014. Satellite remote sensing for applied ecologists: Opportunities and challenges. J. Appl. Ecol. 51, 839–848. https://doi.org/10.1111/1365-2664.12261

Pimm, S.L., Alibhai, S., Bergl, R., Dehgan, A., Giri, C., Jewell, Z., Joppa, L., Kays, R., Loarie, S., 2015. Emerging Technologies to Conserve Biodiversity. Trends Ecol. Evol. 30, 685–696. https://doi.org/10.1016/j.tree.2015.08.008

Pomerantz, A., Peñafiel, N., Arteaga, A., Bustamante, L., Pichardo, F., Coloma, L.A., Barrio-Amorós, C.L., Salazar-Valenzuela, D., Prost, S., 2018. Real-time DNA barcoding in a rainforest using nanopore sequencing: Opportunities for rapid biodiversity assessments and local capacity building. Gigascience 7, 1–14. https://doi.org/10.1093/gigascience/giy033

R Core Team, 2013. R: A language and environment for statistical computer. R Found. Stat. Comput. https://doi.org/10.1007/978-3-540-74686-7

Ripperger, S.P., Carter, G.G., Page Supervision, R.A., Duda, N., Koelpin, A., Weigel, R., Hartmann, M., Nowak, T., Thielecke, J., Schadhauser, M., Robert, J., Herbst, S., Meyer-Wegener, K., Wägemann, P., Preikschat, W.S., Cassens, B., Kapitza, R., Dressler, F., Mayer, F., 2020. Thinking small: Next-generation sensor networks close the size gap in vertebrate biologging. PLoS Biol. 18, 1–25. https://doi.org/10.1371/journal.pbio.3000655

Snaddon, J., Petrokofsky, G., Jepson, P., Willis, K.J., 2013. Biodiversity technologies: Tools as change agents. Biol. Lett. 9, 3–5. https://doi.org/10.1098/rsbl.2012.1029

Speaker, T., O'Donnell, S., Wittemyer, G., Bruyere, B., Loucks, C., Dancer, A., Carter, M., Fegraus, E., Palmer, J., Warren, E., Solomon, J., 2022. A global community-sourced assessment of the state of

conservation technology. Conserv. Biol. 36, 1–13. https://doi.org/10.1111/cobi.13871
Tabak, M.A., Norouzzadeh, M.S., Wolfson, D.W., Sweeney, S.J., Vercauteren, K.C., Snow, N.P., Halseth, J.M., Di Salvo, P.A., Lewis, J.S., White, M.D., Teton, B., Beasley, J.C., Schlichting, P.E., Boughton, R.K., Wight, B., Newkirk, E.S., Ivan, J.S., Odell, E.A., Brook, R.K., et al., 2018. Machine learning to classify animal species in camera trap images: Applications in ecology. Methods Ecol. Evol. https://doi.org/10.1111/2041-210X.13120
Vulcan, 2022. EarthRanger [WWW Document].
Wall, J., Wittemyer, G., Klinkenberg, B., Douglas-Hamilton, I., 2014. Novel opportunities for wildlife conservation and research with real-time monitoring. Ecol. Appl. 24, 593–601. https://doi.org/10.1890/13-1971.1
Weise, F.J., Hauptmeier, H., Stratford, K.J., Hayward, M.W., Aal, K., Heuer, M., Tomeletso, M., Wulf, V., Somers, M.J., Stein, A.B., 2019. Lions at the Gates: Trans-disciplinary Design of an Early Warning System to Improve Human-Lion Coexistence. Front. Ecol. Evol. 6, 242. https://doi.org/10.3389/fevo.2018.00242
Xu, H., Wang, K., Vayanos, P., Tambe, M., 2018. Strategic Coordination of Human Patrollers and Mobile Sensors with Signaling for Security Games 2.
Zárybnická, M., Kubizňák, P., Šindelář, J., Hlaváč, V., 2016. Smart nest box: A tool and methodology for monitoring of cavity-dwelling animals. Methods Ecol. Evol. 7, 483–492. https://doi.org/10.1111/2041-210X.12509

APPENDIX A: SUPPLEMENTARY MATERIALS 'RISK PERCEPTION AND TOLERANCE SHAPE VARIATION IN AGRICULTURAL USE FOR A TRANSBOUNDARY ELEPHANT POPULATION'

1. Tracking and Spatial Data

Table A1. Summaries of data for the 66 elephants included in the study. Fig 1 (main text) shows the GPS locations in the study system. Missing location data averaged 6% across individuals.

Subject name	sex	Age class	DOB	region	# fixes	dataStart	dataStop
Bonchugu	female	young adult	1996	serengeti	16056	3/3/18	12/31/19
Chenga	male	mature adult	1981	serengeti	11016	9/29/18	12/31/19
Chuma	male	young adult	2000	serengeti	16056	3/3/18	12/31/19
Harakati	male	mature adult	1982	serengeti	11016	9/29/18	12/31/19
Imara	male	mature adult	1979	serengeti	16056	3/3/18	12/31/19
Jerahapembe	male	mature adult	1982	serengeti	11016	9/29/18	12/31/19
Jinomoja	female	young adult	1990	serengeti	11016	9/29/18	12/31/19
Kawanga	female	young adult	2003	serengeti	11016	9/29/18	12/31/19
Kimbizwa	male	young adult	1988	serengeti	11016	9/29/18	12/31/19
Kinundu	male	young adult	1990	serengeti	16056	3/3/18	12/31/19
Lowana	male	mature adult	1996	serengeti	15525	3/3/18	12/9/19
Matobo	male	young adult	1993	serengeti	16056	3/3/18	12/31/19
Mchaichai	female	young adult	2001	serengeti	11016	9/29/18	12/31/19
Mchana	female	young adult	1994	serengeti	3131	8/23/19	12/31/19
Mchuri	female	young adult	1994	serengeti	16056	3/3/18	12/31/19
Meru	female	mature adult	1975	serengeti	8811	9/29/18	12/31/19
Mgumu	male	young adult	1991	serengeti	11016	9/29/18	12/31/19
Mgunga	female	young adult	1984	serengeti	15900	3/3/18	12/31/19
Mjerumani	male	young adult	2000	serengeti	11016	9/29/18	12/31/19
Mkomre	female	young adult	1997	serengeti	16056	3/3/18	12/31/19
Mkonga	male	young adult	2001	serengeti	11016	9/29/18	12/31/19
Mtama	female	young adult	1990	serengeti	11016	9/29/18	12/31/19
Mtembezi	male	mature adult	1975	serengeti	11016	9/29/18	12/31/19
Radi	female	mature adult	1981	serengeti	10637	3/3/18	5/20/19
Tai	female	young adult	2001	serengeti	11016	9/29/18	12/31/19
Tarangire	female	young adult	1992	serengeti	11016	9/29/18	12/31/19
Tarime	female	young adult	1996	serengeti	11016	9/29/18	12/31/19
Ukungu	male	mature adult	1971	serengeti	13585	3/3/18	9/20/19
Ukwaju	female	mature adult	1993	serengeti	16056	3/3/18	12/31/19
Vurugu	male	young adult	1989	serengeti	6154	4/19/19	12/31/19
Alina	female	young adult	1991	masai mara	27393	11/10/15	12/26/18

Bobo	male	mature adult	1975	masai mara	15212	3/22/14	6/21/16
Caroline	female	young adult	1986	masai mara	60444	12/10/11	5/8/20
Chelsea	female	young adult	1985	masai mara	42695	5/16/15	6/16/20
Chiri	female	young adult	1996	masai mara	14457	2/2/16	9/27/17
Courtney	female	young adult	1996	masai mara	8345	10/29/16	10/12/17
Fitz	male	young adult	NA	masai mara	8317	8/20/19	8/1/20
Fred	male	mature adult	1975	masai mara	59391	2/2/13	8/1/20
Hangzhou	female	mature adult	1975	masai mara	20541	7/23/17	11/26/19
Hugo	male	mature adult	1972	masai mara	61340	9/5/12	12/5/19
Ivy	female	young adult	1993	masai mara	69516	12/6/11	8/1/20
Jacinta	female	mature adult	1971	masai mara	21553	12/8/11	10/9/14
Kegol	male	mature adult	1978	masai mara	45213	3/4/15	8/1/20
Kenyorra	female	mature adult	1959	masai mara	17236	1/25/16	1/12/18
Kiambi	male	mature adult	1971	masai mara	32632	1/30/16	8/1/20
Kipngetich	female	young adult	1978	masai mara	9152	9/1/12	10/30/13
Lempiris	male	young adult	1987	masai mara	23391	11/10/17	8/1/20
Limo	male	mature adult	1973	masai mara	36634	5/15/15	9/15/19
Lina	female	young adult	1993	masai mara	15378	3/3/14	2/4/16
Lucy	female	young adult	1998	masai mara	19791	4/20/15	9/9/17
Maddy	female	young adult	1988	masai mara	24605	12/5/11	7/6/15
Marima	female	young adult	1985	masai mara	19582	9/28/11	4/7/15
Mytene	male	mature adult	1973	masai mara	40042	6/29/13	4/9/18
Naibosho	female	young adult	1986	masai mara	61691	12/7/11	3/30/20
Namunyak	female	young adult	1981	masai mara	36470	1/27/16	3/26/20
Olchoda	male	mature adult	1980	masai mara	15288	11/9/16	8/8/18
Olenashui	male	mature adult	1968	masai mara	15044	9/22/11	6/24/13
Olopito	female	young adult	1979	masai mara	8883	9/4/12	10/26/13
Omondi	male	mature adult	1974	masai mara	25650	12/9/11	4/19/15
Pepper	male	young adult	1983	masai mara	24743	12/6/11	1/14/15
Polaris	male	mature adult	1970	masai mara	19878	6/28/13	12/28/15
Shorty	male	mature adult	1975	serengeti	39964	6/29/15	8/1/20
Sindiyo	male	mature adult	1976	masai mara	24490	12/7/11	2/1/15
Siyabei	female	young adult	1985	masai mara	7379	9/28/11	8/6/12
Tressa	female	young adult	1986	masai mara	41257	11/12/15	8/1/20
YaoMing	male	young adult	1981	masai mara	5660	12/10/11	1/8/13

Table A2. Spatial covariates used for hidden Markov models. A description of the layer, raster resolution, predicted effect in the model, and the source of the data are provided. Results of the effect of each covariate can be found in Figure S7.

Spatial Covariate	Description	Raster Resolution	Predicted Effect on Probability of Entering Behavioral State (S1/S2/S3)	Source
Distance to Permanent Rivers	Euclidean distance to permanent rivers. Digitized from satellite imagery	30m	(+/+/-)	LandDX Database
Distance to Seasonal Rivers	Euclidean distance to seasonal rivers. Digitized from satellite imagery	30m	(+/+/-)	LandDX Database
Distance to Agricultural	Euclidean distance to agricultural edge	30m	(-/+/+)	Velhuis et al. 2019
Distance to Forest	Euclidean distance to forest edge	30m	(+/+/-)	Landsat8/Google Earth Engine product
Slope	Slope derived from DEM	30m	(+/-/-)	DEM product/Google Earth Engine product
Distance to Primary Roads	Euclidean distance to primary roads. Ground-mapped	30m	(-/-/+)	LandDX Database
Distance to Secondary Roads	Euclidean distance to secondary roads. Ground-mapped	30m	(-/-/+)	LandDX Database
Human Modification	Human Modification Index. Range from 0 to 1 of increasing human modification based on different aspects of human footprint	1000m	(-/-/+)	Kennedy et al. 2019; Google Earth Engine product

2. Agricultural Tactics Clustering

We explored the combination of several metrics for clustering that reflect fluctuation in agricultural use: mean use, maximum use, and the difference between mean and max use. For each individual i, we coded each GPS relocation x in movement track k as inside (1) or outside (0) of agriculture. Mean use for each individual's movement track was calculated as $\overline{x_i} = \frac{1}{N}\sum_{i=1}^{n} x_i$, where n is the total number of points in the track. For maximum use, we calculated a 90-day moving average of agricultural use as $y_i = \frac{1}{W}\sum_{i=n-N+1}^{W} x_i$, where W = window size, and y represents a vector of moving averages for each individual i. A sample of moving window results for 4 individuals are shown in Figure S1. Maximum use was then calculated as max(y_i), representing peak use in the moving average. Difference between mean and max was calculated as the delta between mean and max usage. Summaries of agricultural use metrics for individual elephants are stored in the Dryad Digital Repository: https://doi.org/10.5061/dryad.rn8pk0pbn.

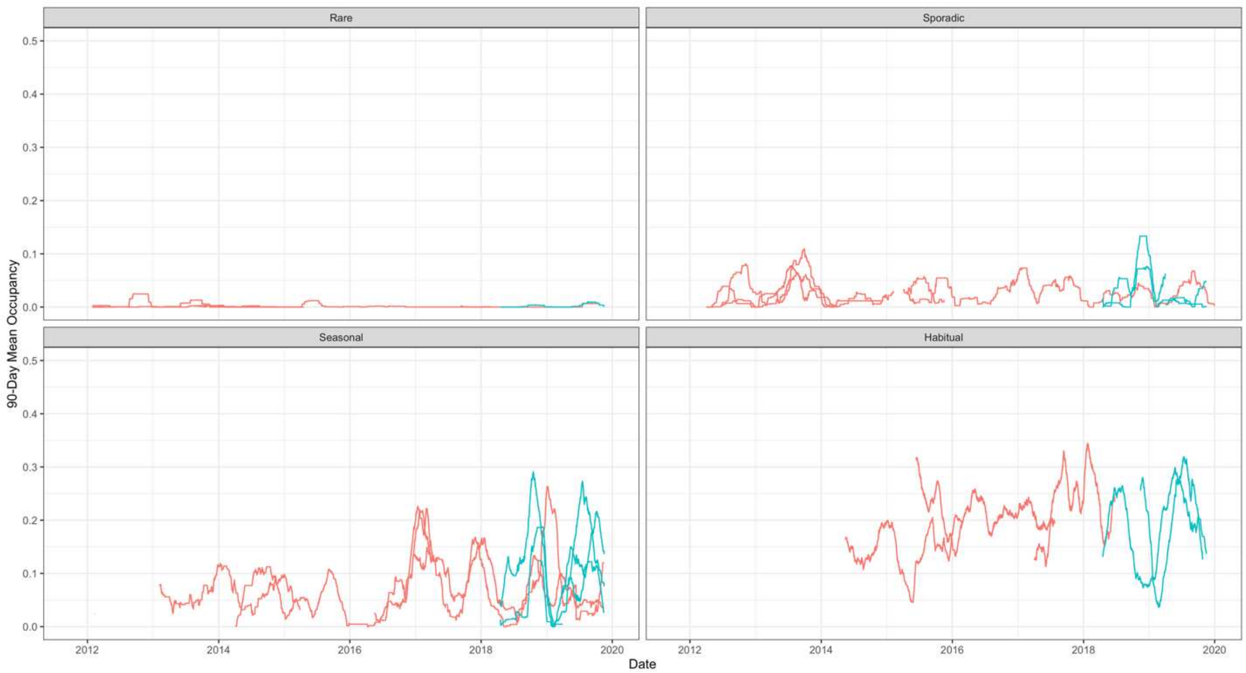

Figure A1. 90-Day moving window plots for a subset of 20 elephants over their multi-year tracking dataset. Time is shown on the x-axis, and percent agricultural use is shown on the y-axis. Plots are faceted by individual-year agricultural use tactic. Crop seasons differ slightly between the Mara and Serengeti regions of the ecosystem. Colors correspond to the elephant's geographic region. Red = Masai mara and blue = Serengeti.

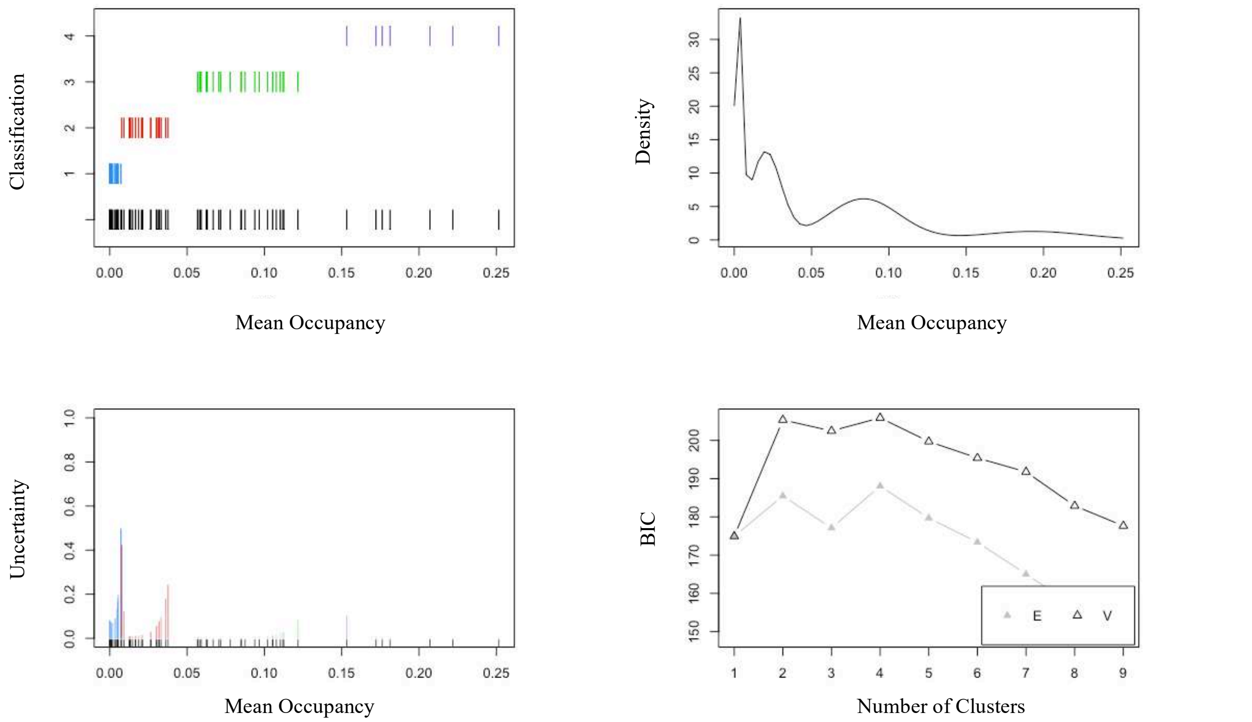

Figure A2. A) Classification results of the mean agricultural use model. Individual black bars represent the 66 individual elephants as a rug plot. Colored bars correspond to 4 clusters denoted on the y axis; B) A density plot of the clusters by mean agricultural use. Higher density corresponds to tighter clusters; C) Uncertainty estimates for each individual's classification. D) BIC results shown with increasing number of clusters, and with two covariance structures.

Table A3. Model selection table for drivers of mean yearly agricultural use. MDD is mean daily displacement calculated by individual year. MCP is minimum convex polygon calculated by individual year.

Model	df	Log Likelihood	AICc	ΔAICc
log(MDD) + log(MCP) + (1|ID)	5	353.50	-696.70	0
sex + log(MDD) + log(MCP) + (1|ID)	7	355.17	-695.75	0.95
log(MDD) + (1|ID)	4	351.79	-695.39	1.31
sex + log(MDD) + log(MCP) + (1|ID)	5	352.35	-694.34	2.36
sex + ageclass + log(MCP) + (1|ID)	6	352.86	-693.29	3.41
log(MCP) + (1|ID)	4	350.67	-693.12	3.58

Table A4. Model selection table for drivers of tactic switching by individuals between years. MCP is minimum convex polygon, and MDD is mean daily displacement.

Model	df	Log Likelihood	AICc	ΔAICc
sex*ageclass + log(MCP) + (1|ID)	6	-77.79	168.23	0
sex*ageclass + (1|ID)	5	-79.43	169.33	1.1
sex + ageclass + (1|ID)	4	-80.83	169.97	1.74
sex + ageclass + log(MDD) + log(MCP) + (1|ID)	7	-77.69	170.26	2.03
sex + ageclass + log(MDD) + (1|ID)	6	-80.59	171.32	3.09

3. Hidden Markov Models

Discrete-time HMMs use speed, turning angle, and other data streams from animal telemetry data to infer latent behavioral states. States are based on step lengths and turning angles where longer more directed steps are clustered distinctly from shorter less directed steps (Fig S3). Following recommendations from McClintock et al. (2013), we filtered GPS relocations to movement tracks with <5% missing data using the adeHabitatLT package in R (Calenge, 2015b). We further excluded movement tracks with <500 relocations, resulting in 54 individuals used for behavioral state estimation.

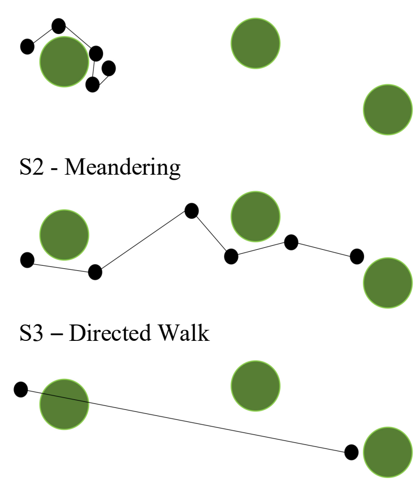

Figure A3. Examples of encamped, meandering, and directed walk movement steps on a landscape. Green circles represent features on the landscape. Black dots represent GPS relocations and lines represent the steps taken between successive relocations.

Model fitting

To initialize the model, behavioral states were parameterized with estimated log speed and turning angles for each state. We used a normal distribution for log speed and a Von Mises distribution for turning angles. To fine tune initialization parameters, we retried fits on a null three-state model with no covariates to optimize the parameters. Models were not sensitive to changes, as assessed by log likelihood and the fitted model estimates of state-level turning angle and step length distributions. Using the initialization parameters obtained from null model fitting, a candidate set of three-state models was constructed and fit to the data. The HMM determines the probability of switching between the three latent states by estimating a 3x3 transition matrix of transition probabilities between each state. Environmental data can be included as covariates in a linear regression applied to each element of the matrix to improve state estimates. To assess these regressions, candidate models were evaluated using AIC model selection procedures (Table A5).

Table A5. Candidate models for the HMM showing the regression formulas used on the transition matrix, log likelihood, and AIC values used for model selection.

Model	**Log Likelihood**	**AIC**	**ΔAIC**
Dist2ag^2 + Dist2forest + dist2permwater + dist2seasonalwater + humanMod + slope + (1|ID)	-2324333	4648784	0
Dist2ag^2 + dist2permwater + dist2seasonalwater + humanMod + slope + (1|ID)	-2324392	4648890	106
dist2ag + dist2forest + dist2permwater + dist2seasonalwater + humanMod + slope	-2324396	4648898	114
dist2ag + dist2forest + dist2permwater + humanMod + slope	-2324483	4649061	276
dist2ag + dist2forest + dist2permwater + dist2seasonalwater + slope	-2324741	4649576	791

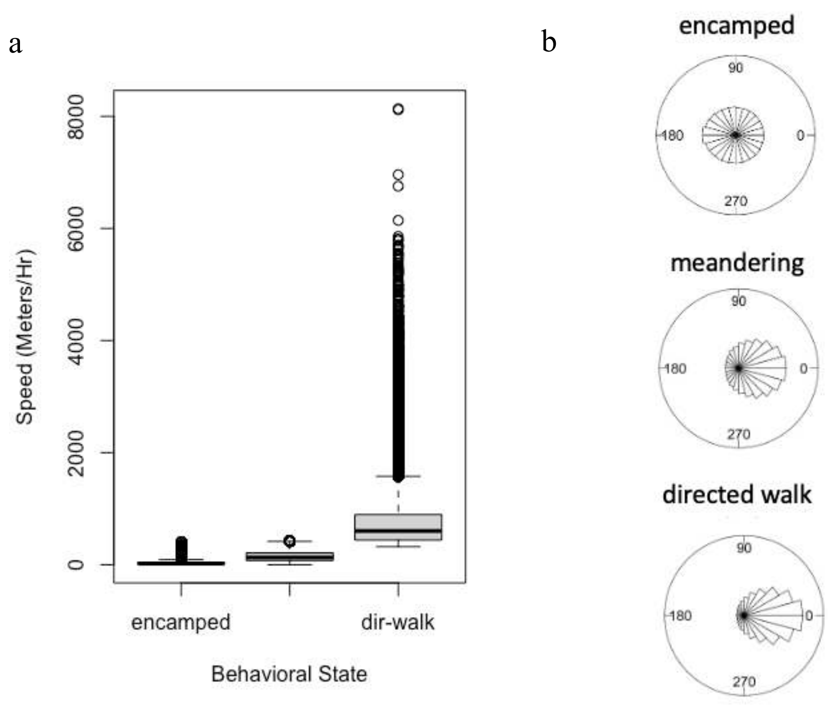

Figure A4. Distribution of step length and turning angle for each state classified by the HMM. A) Boxplots show the distribution of speeds for each state in meters per hour. B) Rose diagram plots show the distribution of turning angle values for each state. Tortuosity is highest with encamped, and lowest in directed walk. 180 degree turning angle corresponds to a reverse in direction from the previous step, and 0 degree turning angle represents no change in direction from the previous step.

A simulation analysis was used to assess the model's ability to recreate the movement process based on step length and turning angles. 100,000 observations were simulated using the transition probability matrix produced from the top model and the simulation function in the MomentuHMM package. Step length and turning angle distributions from the simulated data were evaluated in comparison to the original data. To assess the ability of the model to capture and reproduce the movement process, we compared distributions of step lengths and turning angles for all relocations, and by behavioral state. We detected no large variations between the observed and simulated data (Fig S5).

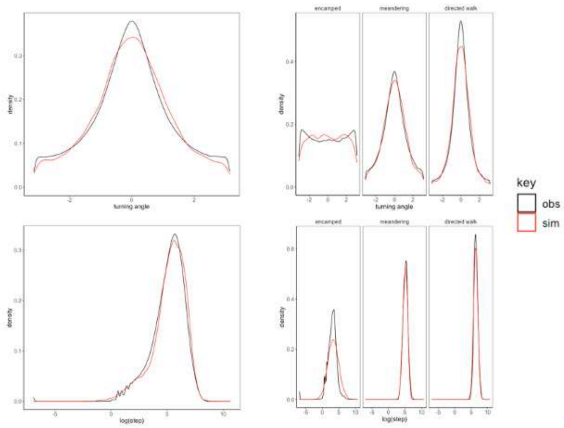

Figure A5. Density distributions from the observed and simulated tracking data. The top row shows turning angle distributions for all relocations, and faceted by behavioral state. The bottom row shows log(step length) distributions. Black lines correspond to observed data, while red lines correspond to simulated data.

4. Activity Budget Density Estimates and Agricultural Use

The Viterbi algorithm was used to estimate the most likely sequence of states from each individual's movement track using the transition probability matrix and observed environmental covariate values, giving us behavioral state estimations for each GPS relocation. From the estimates, we constructed activity time budgets and kernel density estimates of each behavioral state on a 24-hour scale.

To evaluate the effect of environmental covariates on state, stationary state probabilities were produced in relation to each covariate. These probabilities are interpreted as the probability of being in each of the three states in relation to a single covariate, with all other covariates held at their mean value (Figure S6).

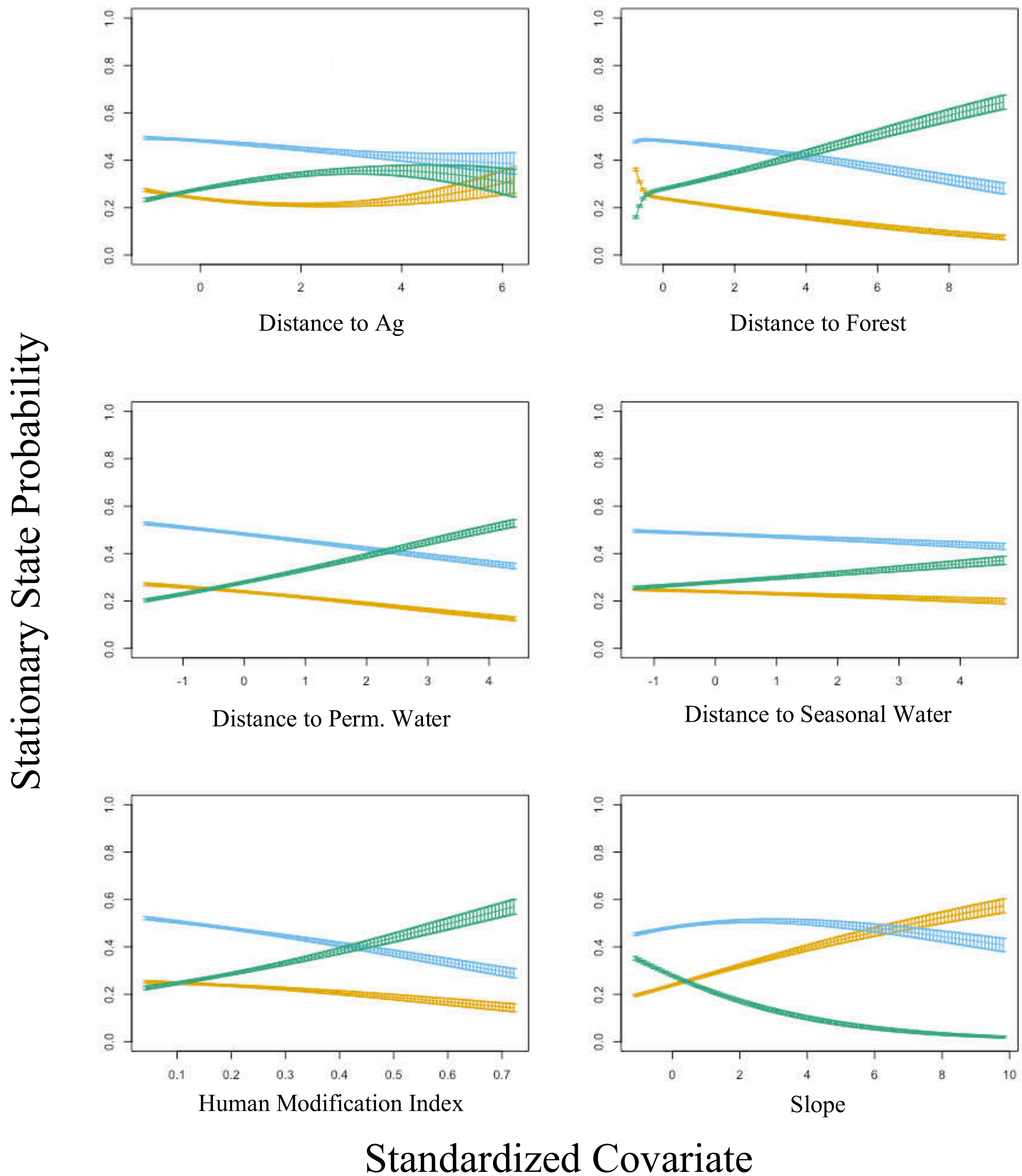

Figure A6. Stationary state probabilities and 95% confidence intervals for each of the six covariates used in the HMM. Colors correspond to the three states (yellow = encamped, blue = meandering, green = directed walk). The x-axis corresponds to the standardized covariate value, and the y-axis corresponds to the mean probability of being in a state as a function of the covariate, with all other covariates held at their mean value.

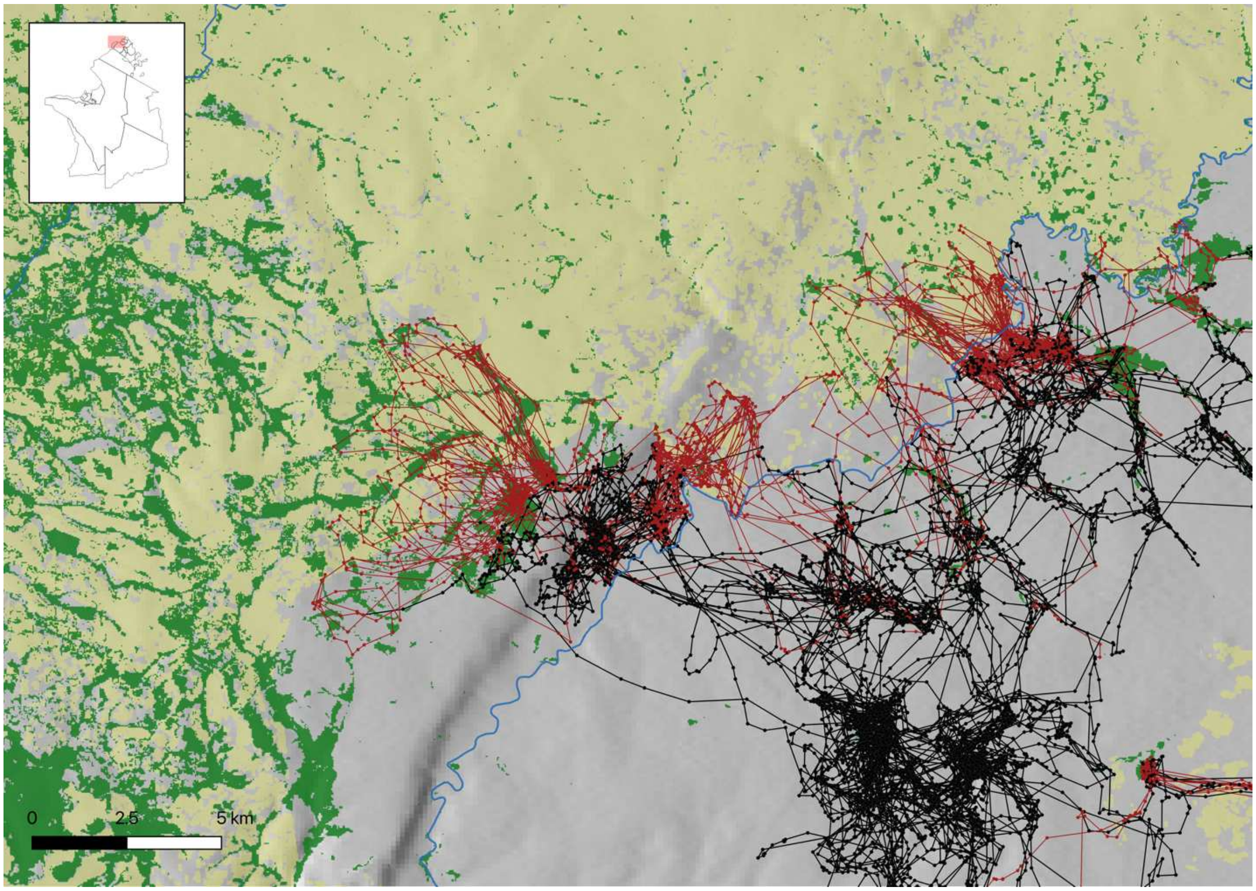

Figure A7. GPS relocations of the elephant Ivy coded by agricultural use phase show crop raiding forays into agricultural land. Phases were defined as relocations within 6 hours (before or after) use agricultural. Red corresponds to agricultural use phases. Black corresponds to non-agricultural use phases. Thick black lines correspond to conservancy borders in the Mara.

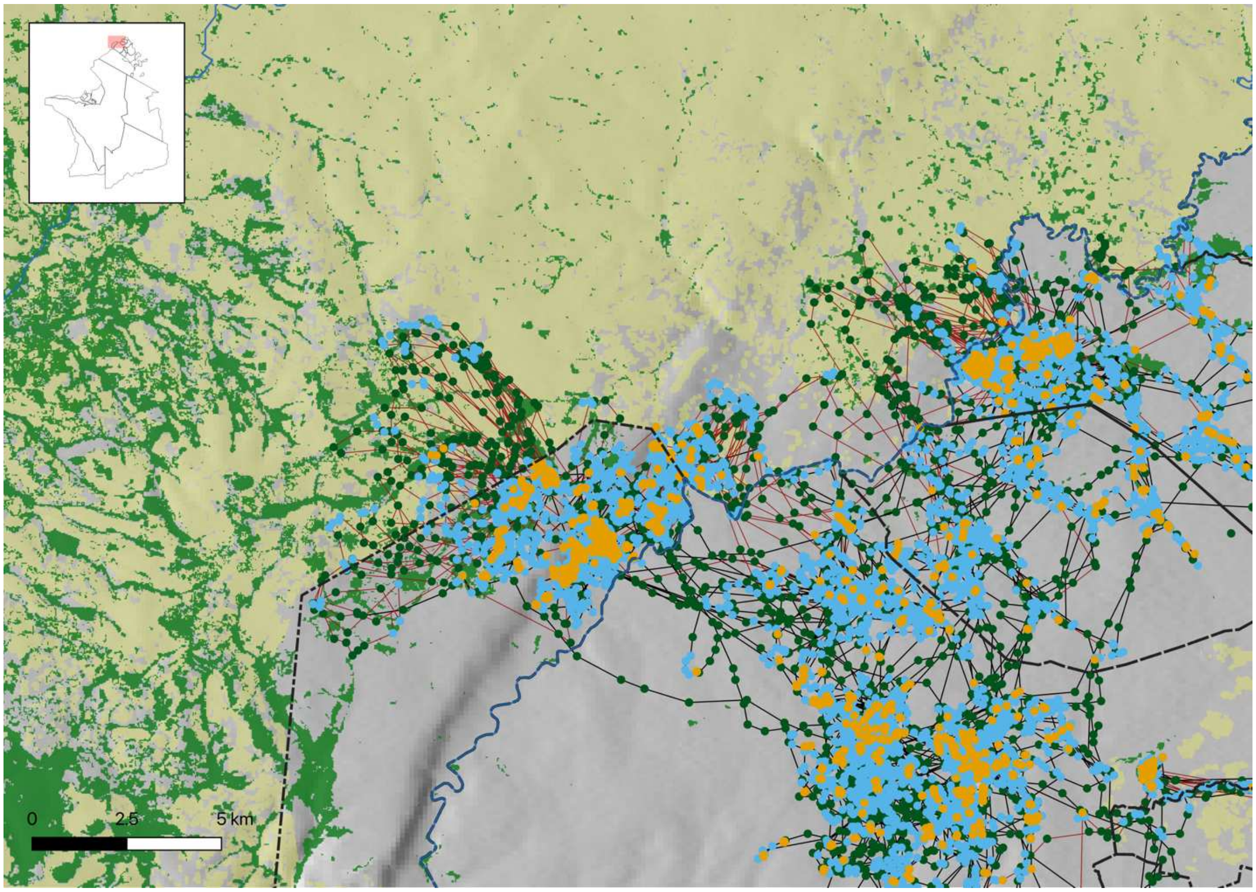

Figure A8. GPS relocations of a single individual, coded by behavioral state and agricultural use phase. Behavioral state is coded by relocation points: orange = encamped, blue = meandering, green = directed walk. Agricultural use phase is coded by trajectories: red = use, black = non-use.

APPENDIX B: SUPPLEMENTAL MATERIALS FOR 'STAGING BEHAVIORS IDENTIFY SPATIAL AND TEMPORAL RISK OF HUMAN-WILDLIFE CONFLICT'

1. Metric Descriptions

To define staging events, metric values were calculated for each unique time window between 6am and 9pm (n = 120), and algorithm permutations were used to test the parameter space of each metric. The parameter space range of each metric was defined by taking the lowest value and third quartile, or highest value and first quartile of the daily mean metric value. We defined mean step length as the mean segment length L off all segments within the time window, where smaller values correspond to less displacement. We assumed that staging would be associated with lower mean step lengths and tested the parameter space from 1 to 1000m, where 1000m was the third quartile of daily mean step length. We defined the straightness index as log(R/L), where R is net displacement and L is the segment length in a given time window (Benhamou, 2004), and smaller values indicate less straight movements. We assumed that staging would be associated with lower straightness index values and tested the parameter space from -1 to 0.01, where 0.01 was the third quartile of daily straightness index. We defined tortuosity as $\log(L/R^2)$, where L is the segment length in a given time window and R is the net displacement (Whittington et al., 2004) and larger tortuosity values correspond to circuitous movements. We assumed that staging would be associated with higher tortuosity values and tested the tortuosity parameter space from 2 to -7, where 2 was the maximum tortuosity value in the dataset and -7 represented the first quartile of mean daily tortuosity in the dataset. We calculated hourly persistence velocity as speed*cos(absolute turning angle) for each segment length (Seidel et al., 2018), and calculated the mean persistence velocity within each time window. Lower persistence velocity values correspond to more embedded movement with lower speeds and more turning, and limited the parameter space from 0 to 400, where 400 was the third quartile of mean daily hourly persistence velocity. The behavioral state definition was conducted as described in Hahn et al., 2021, and uses a combination of speed and turning angle to classify each movement step into one of three states (encamped, meandering, and directed walk) using hidden Markov models, where encamped behavior corresponds to low speeds and increased turning. We assumed that encamped behavior was characteristic of staging and calculated the percentage of encamped relocations within the time window (parameter space of 0 to 1).

2. Tables & Figures

Table B1. Omission-commission results from ensemble algorithm outputs for all tested movement metrics. Omission is the percentage of agricultural use days that were not detected using the staging algorithm (false negative). Commission is the percentage of non-agricultural use days that were classified as agricultural stages by the algorithm (false positive). Values are reported as percentages. See Table 1 for metric descriptions.

Metric	Type	Movement Only	Ag Filter
Step Length	Omission	0.06	0.29
	Commission	0.49	0.48
HMM Behavioral State	Omission	0.36	0.37
	Commission	0.44	0.35
Net Displacement	Omission	0.8	0.81
	Commission	0.38	0.29
Tortuosity	Omission	0.13	0.17
	Commission	0.49	0.3
Straightness Index	Omission	0.63	0.64
	Commission	0.50	0.34
Persistence Velocity	Omission	0.20	0.39
	Commission	0.48	0.46

Table B2. Model selection table for the generalized logistic mixed effects regression of staging propensity defined by tortuosity. All models include a random effect for subject ID. AC corresponds to the autocovariate term. HF represents human footprint. A description of all covariates and their preparation can be found in the methods section.

Terms	df	logLik	AICc	delta	weight
prop.forest.250 + prop.ag.1500 + HM + slope + dist2paedge + drains.250 + AC	9	-47450.57	94919.14	0	0.99978
prop.forest.250 + prop.ag.1500 + HM + slope + drains.250 + AC	8	-47459.98	94935.97	16.826	0.00022
prop.forest.250 + prop.ag.1500 + HM + slope + dist2paedge + AC	8	-47551.15	95118.3	199.15	5.68E-44
prop.forest.250 + prop.ag.1500 + HM + slope + AC	7	-47559.29	95132.59	213.45	4.47E-47
prop.forest.250 + slope + drains.250 + AC	7	-47624.48	95262.96	343.81	2.20E-75

Table B3. Model selection table for generalized logistic mixed effects regression of staging propensity defined by behavioral state. All models include a random effect for subject ID. AC corresponds to the autocovariate term. HF represents human footprint. A description of all covariates and their preparation can be found in the methods section.

Terms	df	logLik	AICc	delta	weight
prop.forest.250 + prop.ag.1500 + HM + slope + dist2paedge + drains.250 + AC	9	-26930.603	53879.208	0.000	0.998
prop.forest.250 + prop.ag.1500 + HM + slope + drains.250 + AC	8	-26941.946	53899.893	12.430	0.002
prop.forest.250 + prop.ag.1500 + HM + slope + dist2paedge + AC	8	-26944.870	53905.742	20.686	0.000
prop.forest.250 + prop.ag.1500 + HM + slope + AC	7	-26950.761	53915.523	36.316	0.000
prop.forest.250 + slope + drains.250 + AC	6	-26958.700	53929.402	50.194	0.000
prop.forest.250*HM + prop.ag.1500 + dist2paedge + AC	8	-27038.447	54092.895	181.322	0.000
prop.forest.250 + prop.ag.1500 + HM + slope + drains.250 + AC	7	-27053.325	54120.650	191.655	0.000

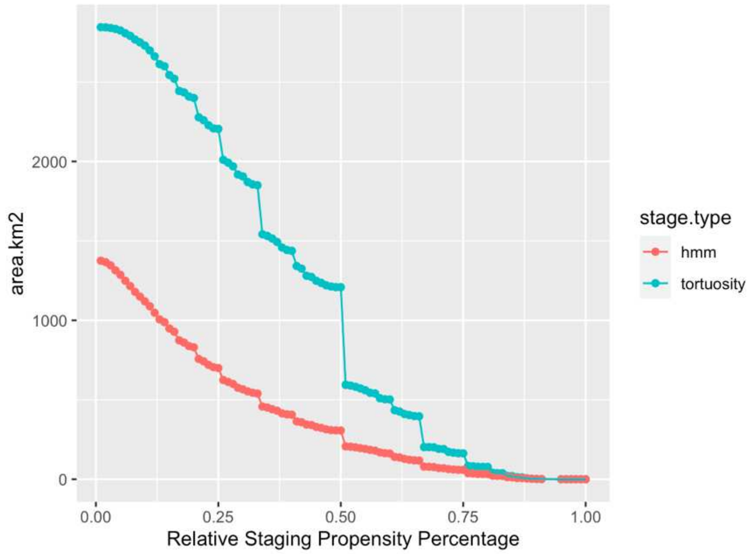

Figure B1. Cumulative area covered by staging clusters with a decreasing threshold of staging propensity. Staging propensity is calculated as staging locations/all agricultural-use day locations on a 250m grid. A threshold appears to occur around 50% (i.e. 50% of locations in a pixel are part of staging events).

3. References

Appelhans, T., Detsch, F., Reudenback, C., Woellauer, S., 2022. mapview: Interactive Viewing of Spatial Data in R.

Benhamou, S., 2004. How to reliably estimate the tortuosity of an animal's path: Straightness, sinuosity, or fractal dimension? J. Theor. Biol. 229, 209–220. https://doi.org/10.1016/j.jtbi.2004.03.016

Hahn, N.R., Wall, J., Denninger-Snyder, K., Goss, M., Sairowua, W., Mbise, N., Estes, A.B., Ndambuki, S., Mjingo, E.E., Douglas-Hamiliton, I., Wittemyer, G., 2021. Risk perception and tolerance shape variation in agricultural use for a transboundary elephant population. J. Anim. Ecol. 91, 112–123. https://doi.org/10.1111/1365-2656.13605

Seidel, D.P., Dougherty, E.R., Carlson, C.J., Getz, W.M., Seidel, D.P., Carlson, C.J., Spiegel, O., Getz, W.M., Dougherty, E.R., Carlson, C.J., Getz, W.M., 2018. Ecological metrics and methods for GPS movement data. Int. J. Geogr. Inf. Sci. 32, 2272–2293. https://doi.org/10.1080/13658816.2018.1498097

Whittington, J., St. Clair, C.C., Mercer, G., 2004. Path tortuosity and the permeability of roads and trails to wolf movement. Ecol. Soc. 9. https://doi.org/10.5751/ES-00617-090104

APPENDIX C: SUPPLEMENTARY MATERIALS FOR ‘CROP USE STRUCTURES RESOURCE SELECTION STRATEGIES IN A HUMAN-DOMINATED LANDSCAPE’

1. Tables

Table C1. Coefficient estimates are shown for the spatially explicit crop selection model. ‘ag’ indicates the crop covariate and ‘buffer’ indicates the buffer level. Brackets indicate the buffer level (e.g. 1000 = less than 1000m from protected areas). Area Under Curve (AUC) values are reported for each of the four models as a measure for goodness-of-fit.

Season	Region	term	estimate	std error	lwr.95	upr.95	AUC
Dry	Masai Mara	ag	-0.74	0.029	-0.796	-0.684	0.72
		buffer[1000]	0.198	0.008	0.182	0.213	
		buffer[2000]	-0.283	0.01	-0.303	-0.264	
		buffer[3000]	-0.028	0.01	-0.048	-0.008	
		ag:buffer[1000]	0.192	0.039	0.115	0.269	
		ag:buffer[2000]	0.535	0.043	0.451	0.619	
		ag:buffer[3000]	0.051	0.049	-0.045	0.148	
	Serengeti	ag	-0.892	0.021	-0.932	-0.852	0.76
		buffer[1000]	1.181	0.012	1.157	1.204	
		buffer[2000]	0.86	0.013	0.833	0.886	
		buffer[3000]	0.564	0.015	0.534	0.593	
		ag:buffer[1000]	0.401	0.024	0.354	0.448	
		ag:buffer[2000]	0.264	0.026	0.212	0.316	
		ag:buffer[3000]	0.171	0.03	0.113	0.23	
Wet	Masai Mara	ag	-0.327	0.04	-0.405	-0.249	0.59
		buffer[1000]	-0.525	0.013	-0.552	-0.499	
		buffer[2000]	-0.826	0.017	-0.86	-0.793	
		buffer[3000]	-0.122	0.016	-0.152	-0.091	
		ag:buffer[1000]	-0.074	0.068	-0.207	0.058	
		ag:buffer[2000]	0.231	0.078	0.078	0.384	
		ag:buffer[3000]	-0.052	0.077	-0.202	0.098	
	Serengeti	ag	-0.704	0.039	-0.78	-0.628	0.61
		buffer[1000]	0.597	0.025	0.547	0.646	
		buffer[2000]	0.355	0.029	0.299	0.412	
		buffer[3000]	0.202	0.032	0.139	0.265	
		ag:buffer[1000]	0.423	0.046	0.334	0.513	
		ag:buffer[2000]	0.197	0.051	0.097	0.298	
		ag:buffer[3000]	0.158	0.059	0.043	0.274	

APPENDIX D: SUPPLEMENTARY MATERIALS FOR 'IDENTIFYING CONSERVATION TECHNOLOGY NEEDS, BARRIERS, AND OPPORTUNITIES

1. Tables & Figures

Table D1. Model selection results for the model of factors affecting collaboration. Model selection showed the poor collaboration and high cost were the most important factors affecting collaboration ratings. PC = Poor Collaboration, HC = High Cost, LT = lack of technical support, MD = misunderstanding of deliverables, DT = delayed timeline.

Covariates	Covariate Dropped	AICc	logLik	df
PC+HEC+LT+MD+DT+collab.size +tech.type	-	136.292845	-55.32591	10
PC+HC+LT+MD+DT+collab.size	technology type	133.422648	-55.461324	9
PC+HC+LT+MD+DT	collaboration size	131.086468	-55.787136	8
PC+HC+LT+MD	delayed timeline	128.948941	-56.141137	7
PC+HC+LT	misunderstanding of deliverables	127.591812	-56.819162	6
PC+HC	lack of technical support	127.080325	-57.858344	5
PC	high cost	128.495761	-59.803436	4

Table D2. Codes, definitions, example quotes, and code frequencies from theme analysis of answers to the open-ended survey question "Assuming unlimited funding and resources, what technological solution would you want to see developed?" Responses are coded into different themes representing desired applications.

Codes	Definition	Example Quote	Code Frequency
Data Integration	Tools for processing large volumes of data, analytical tools for integrating multiple data sources, integrating drones with GPS collars, and integrating collar data with modelling	"software facilitating better data integration; specifically computational power and tools to integrate and process large volumes of data easily; user friendly tools for developing deep-learning and machine learning analysis"	6
Ecosystem Monitoring	Automated image processing to detect land use change for conservation management, to quantify river discharge, or collect polarized light measurements	"Suite of tools for protected area management, streamlined. Allow countries / PAs to get a higher resolution picture of the ecosystem conditions and ecosystem service valuation of their regions"	9
Animal Image Processing	Automated species or individual animal identification from	"automated image processing for detecting animals in	29

	sensors ; distance to animal measurements, measures of weight/mass, bait detection	satellite and drone imagery"; "automated species recognition & individual ID on camera traps"; "ability to estimate density from camera traps for non-uniquely marked individuals"; "a device to record the mass of individual animals that pass in front of camera traps"; "AI that can recognize bait in camera traps"; "measurement of physiological variables in camera traps"	
Individual-level Monitoring	Improvements to animal tracking devices and adaptations to measure individual animal behaviour and physiology	"Miniaturized animal tracking technologies with extended battery life;" "camera system on animals which links to automated behaviour software"	24
Field Assays and Sample Collection	sex assays from swabs, hormone analysis of samples, field-ready genetic analysis, dietary information from terrestrial vertebrate faecal isotope data, tool to collect hair samples and protect from moisture/weather; tag attachment/retrieval options that do not require capture and immobilization; tool to explore burrows; thermal nest cameras; stereo cameras for 3D wildlife images	"ID animals instantly as male/female from swabs/test strips"; "rapid hormone analysis"; "Near real time dietary information from faecal isotope data"; "mechanism to collect hair samples for DNA analysis that would also protect those samples from moisture"; "Automated on-site parasite identification and quantification portable device"	9

Table D3. Codes, example quotes, and code frequencies of desired improvements to existing technologies derived from a theme analysis of answers to the open-ended survey question "Assuming unlimited funding and resources, what technological solution would you want to see developed?"

Improvements of Existing Technology	**Example Quote**	**Code Frequency**
Affordable	"Soundscape monitoring; tracking animals in a feasible manner, ie., accessible for researchers with less access to funds"	10
Automated	"Automated identification of individual animals based on spot/stripe patterns"; "Automated integration of collaring data with habitat suitability modelling"; "automated drone mapping of all river/stream habitats with LiDAR/sonar"	26
Durable, weatherproof, waterproof	"Better waterproofing for most of the technology we use"; "Sand-proof DSLR cameras"; "Collars with better battery life & collar straps"	8
Self-powered/energy harvesting	"Remotely deployable solar GPS tags"; "Energy harvesting smart cameras with long range connectivity"	4
High quality or high resolution	"good camera trap which will be small as GoPro8 and will produce high quality 10 MP pictures with high iso and will last half year in the field"; "Cameras that triggered faster and with greater sensitivity"; "More sensitive acoustic sensors (enhanced range of detection)"	10
Long battery life	"Drones that can monitor a conservation area for hours. This means a long lasting btterylife"; "Increased battery life for underwater cameras"	8
Non-invasive	"less invasive tracking devices"; "non-invasive genetic analysis in the field"; "Noninvasive aerial insect monitoring"	7
Real-time	"ID animals instantly as male/female from swabs/test strips"; "Mesh network telemetry tags and receivers(real-time, lowest power/kilobyte): tag/receiver proximity measurements, tags as mobile environmental sensors, data storage and forwarding from tags outside the receiver network)"	9
Smaller or Lighter	"miniaturized tracking tag/collars"; "smaller, high-resolution all-weather camera traps"	13
User-friendly	"user friendly tools for developing deep-learning and machine learning analysis"; "easy to implement VHF triangulation systems"	4
Wireless or remote connectivity	"Better data connectivity from the field" ;"improved cell phone, smartphone, and network access for communities living around wildlife conservancies; particularly in developing / low-income regions"; "B.A.T.M.A.N. (Better Approach to Mobile Ad-hoc Networking) for LoRa"	12

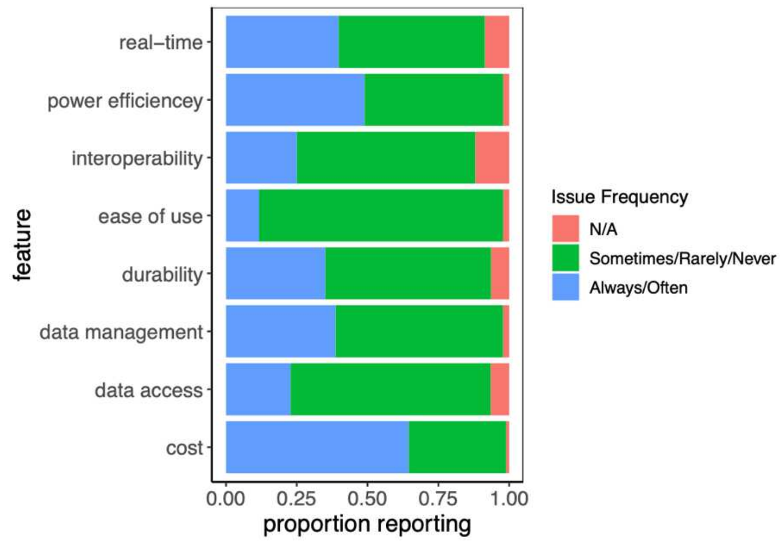

Figure D1. Summary of responses to the question "How often do you encounter technical issues with each of the following technology features?". To summarize the data, the frequency of feature issues are condensed into three categories: Always/Often, Sometimes/Rarely/Never, and Not Applicable. Based on these categories, over 50% of respondents experience issues always or often with every feature. Cost is the most frequent issue (77% always/often), but is also the most commonly reported as not applicable (16%). Issues with power efficiency (73% always/often) and durability (69%) were also common.

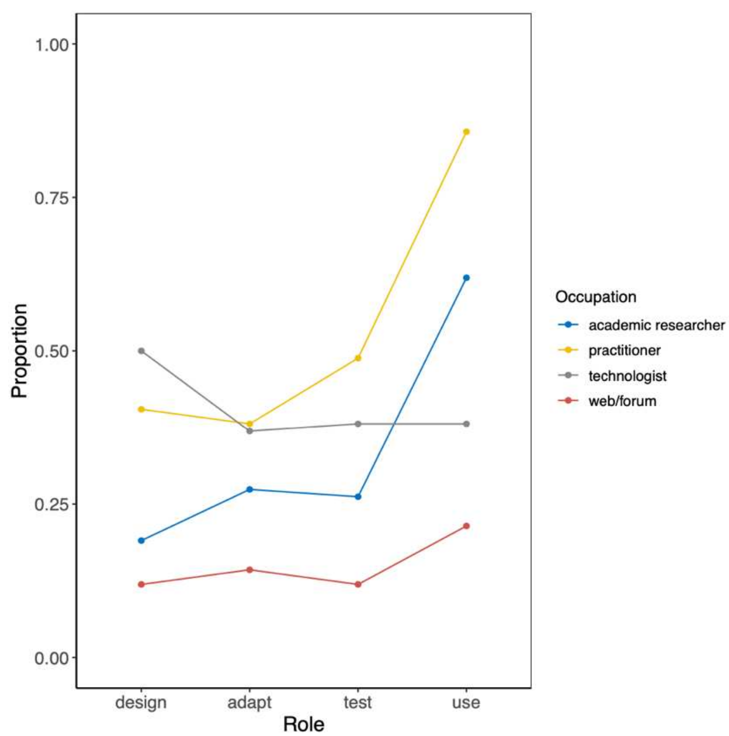

Figure D2. Rates of participation in collaborations within each role of the development process. Each colored line corresponds to a different collaborator type. We asked about websites and forums to distinguish when collaborations were turning to online resources and documentation for technical support as opposed to technologists.

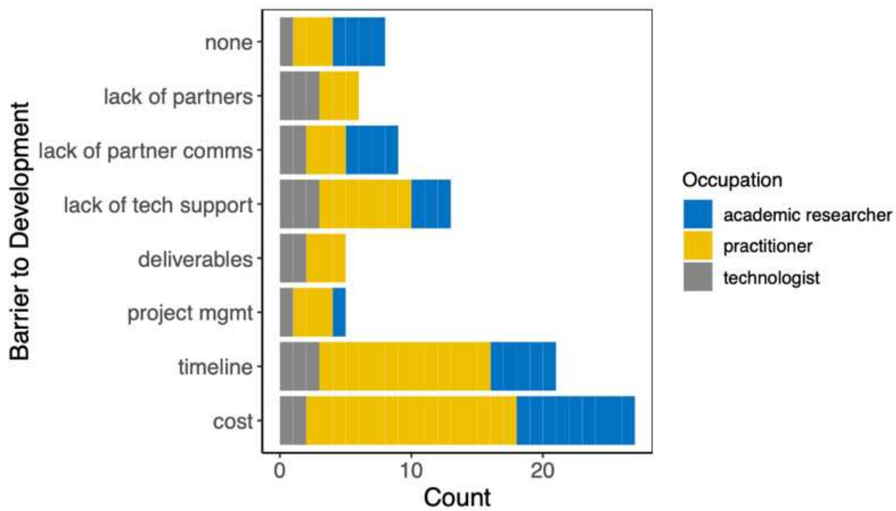

Figure D3. Summary of responses to the question 'What barriers do have you experienced in developing conservation technologies?". High cost, delayed time-line, and lack of technical support are the three most commonly-reported barriers.

2. Survey Instrument

Tech Familiarity

For this survey, technology is defined as any device or software that is used to help conduct research, management, and other conservation-related activities.

Please answer questions based on your last 5 years of experience.

How familiar are you with the use of technology (e.g. camera traps, machine learning, remote sensing) in conservation research and practice?

- ○ Not familiar at all
- ○ Slightly familiar
- ○ Moderately familiar
- ○ Very familiar
- ○ Extremely familiar

Horizon Scan

Are there any technological advances, tools, or devices that do not exist, but if developed would allow you to address novel research questions or create new conservation solutions in your field?

- ○ Yes
- ○ No

What research or conservation need would the technological solution fill?

- ☐ Species monitoring
- ☐ Ecosystem monitoring
- ☐ Real-time monitoring
- ☐ Automated processing
- ☐ Data integration/visualization
- ☐ Law enforcement
- ☐ Physical asset management
- ☐ ______ Other

Assuming unlimited funding and resources, what technological solution would you want to see developed?

Biodata

Biodata

How would you best describe your position/role?

- ○ Front-lines conservationist
- ○ Conservation facilitator
- ○ Researcher (non-academia)
- ○ Professor/Faculty/Postdoc
- ○ Graduate student
- ○ Technologist
- ○ [ ] Other

Main country(s) of work. List up to three.

Country 1 [ ]

Country 2 [ ]

Country 3 [ ]

What biomes represent your main location of study/work? Select all that apply.
Hold down ctrl (Windows) or cmd (Mac) to select multiple.

Terrestrial
- Tropical Rainforests
- Temperate Forests
- Taiga
- Deserts
- Grasslands
- Savanna
- Tundra
- Urban/Periurban

Wetlands

What best describes your conservation focus? Select all that apply.
Hold down ctrl (Windows) or cmd (Mac) to select multiple.

Research
- Applying/developing research methods
- Biodiversity surveys & mapping species distributions
- Conservation management (implementing or evaluating)
- Conservation planning for species or conservation areas
- Study of species biology
- Wider context of conservation

Threats to Biodiversity
- Climate change
- Disturbance

What best describes your research focus? Select all that apply.
Hold down ctrl (Windows) or cmd (Mac) to select multiple.

Species
- Birds
- Mammals
- Fish
- Reptiles
- Invertebrates
- Amphibians
- Plants
- Bacteria, archaebacteria, fungi, protozoa

Wildlands/Landscapes Conservation

What best desribes the organization that you work for?

○ Conservation NGO
○ Collaborative research partnership/Institute
○ Government agency
○ University
○ Technology company
○ [ ] Other

Years of experience in your field. Field refers to the field most related to your use of conservation technology.

○ 0-4 years
○ 5-9 years
○ 10-14 years
○ 15+ years

If you found this survey to be valuable and would like to send it to others, please add contact email addresses here. We will add them to our distribution list.

[ ]

Default Question Block

How have you interacted with conservation/research-centric technology? Select all that apply.

- ☐ Use of technology in the field: use of existing/established tech
- ☐ Adaptation of existing technologies: modifications of existing tech to suit conservation use cases
- ☐ Development of new technologies: creating new tech for conservation use cases
- ☐ Testing of new/adapted technology: trialing of new/unproven tech
- ☐ Participation in technology challenges or outreach
- ☐ I have not interacted directly with conservation technologies

How often do you experience the following technical and performance issues while using technology for conservation research and practice?
For statements that are not applicable to your work, indicate N/A.

	How often do you experience this issue?						Has this issue ever prevented you from using a technology? Click if yes
	N/A	Never	Rarely	Sometimes	Often	Always	Select all that apply
Lack of durability/field-proofing (e.g. theft, waterproofing)	○	○	○	○	○	○	☐
Difficulty of use	○	○	○	○	○	○	☐
Lack of real-time data/connectivity	○	○	○	○	○	○	☐
High cost	○	○	○	○	○	○	☐
Limited power efficiency/battery life	○	○	○	○	○	○	☐
Data access/sharing limitations	○	○	○	○	○	○	☐
Data management challenges	○	○	○	○	○	○	☐
Limited interoperability with existing tools and workflows	○	○	○	○	○	○	☐
Other ______	○	○	○	○	○	○	☐

What are the technology tools that you/your team use for collecting data and implementing conservation activities?
To select multiple technologies, hold down ctrl (Windows) or cmd (Mac).

Sensors/Hardware
- Camera traps
- Acoustic sensors
- Tracking tags/collars
- Solar power source equipment
- Cell phone
- Handheld GPS
- UAVs/Drones
- Digital/DSLR cameras
- Seismic sensors

Other

Indicate how you use each technology in conservation settings.

	What application do you use this technology for? Select all that apply.						
	Species Monitoring	Ecosystem Monitoring	Real-time Monitoring	Automated Processing	Data Integration/Visualization	Law Enforcement	Physical Asset Management
» Camera traps	☐	☐	☐	☐	☐	☐	☐
» Acoustic sensors	☐	☐	☐	☐	☐	☐	☐
» Tracking tags/collars	☐	☐	☐	☐	☐	☐	☐
» Solar power source equipment	☐	☐	☐	☐	☐	☐	☐
» Cell phone	☐	☐	☐	☐	☐	☐	☐
» Handheld GPS	☐	☐	☐	☐	☐	☐	☐
» UAVs/Drones	☐	☐	☐	☐	☐	☐	☐
» Digital/DSLR cameras	☐	☐	☐	☐	☐	☐	☐
» Seismic sensors	☐	☐	☐	☐	☐	☐	☐
» 3D Printing	☐	☐	☐	☐	☐	☐	☐
» Low resolution satellite imagery (10+ meter)	☐	☐	☐	☐	☐	☐	☐
» High resolution satellite (sub-10 meter)	☐	☐	☐	☐	☐	☐	☐
» Multispectral	☐	☐	☐	☐	☐	☐	☐
» Thermal	☐	☐	☐	☐	☐	☐	☐
» LiDAR	☐	☐	☐	☐	☐	☐	☐
» Radar	☐	☐	☐	☐	☐	☐	☐
» Machine learning/AI	☐	☐	☐	☐	☐	☐	☐
» Mobile survey platforms (e.g., survey123)	☐	☐	☐	☐	☐	☐	☐
» Imagery processing platforms (e.g. Google Earth Engine)	☐	☐	☐	☐	☐	☐	☐
» Image processing tools (e.g. camera trap labeling)	☐	☐	☐	☐	☐	☐	☐
» Automated image processing tools (e.g. AI-based species ID)	☐	☐	☐	☐	☐	☐	☐
» Audio processing tools	☐	☐	☐	☐	☐	☐	☐
» Automated audio processing tools	☐	☐	☐	☐	☐	☐	☐
» eDNA/Metabarcoding	☐	☐	☐	☐	☐	☐	☐
» Field forensics kits	☐	☐	☐	☐	☐	☐	☐
» Satellite communication	☐	☐	☐	☐	☐	☐	☐

	What application do you use this technology for? Select all that apply.						
	Species Monitoring	Ecosystem Monitoring	Real-time Monitoring	Automated Processing	Data Integration/Visualization	Law Enforcement	Physical Asset Management
» LoRa	☐	☐	☐	☐	☐	☐	☐
» Radio	☐	☐	☐	☐	☐	☐	☐
» Other	☐	☐	☐	☐	☐	☐	☐

Use the matrix to evaluate the frequency of use and performance of each technology.

	How often do you use this technology?	How would you evaluate the overall performance of this technology?
» Camera traps		
» Acoustic sensors		
» Tracking tags/collars		
» Solar power source equipment		
» Cell phone		
» Handheld GPS		
» UAVs/Drones		
» Digital/DSLR cameras		
» Seismic sensors		
» 3D Printing		
» Low resolution satellite imagery (10+ meter)		
» High resolution satellite (sub-10 meter)		
» Multispectral		
» Thermal		
» LiDAR		
» Radar		
» Machine learning/AI		
» Mobile survey platforms (e.g., survey123)		
» Imagery processing platforms (e.g. Google Earth Engine)		
» Image processing tools (e.g. camera trap labeling)		
» Automated image processing tools (e.g. AI-based species ID)		
» Audio processing tools		
» Automated audio processing tools		
» eDNA/Metabarcoding		
» Field forensics kits		
» Satellite communication		
» LoRa		
» Radio		
» Other		

What types of collaborators do you work with to use technologies in conservation research and practice? Select all that apply.
Hold down ctrl (Windows) or cmd (Mac) to select multiple.

Conservation Partners
- Field-based/local conservation group
- International conservation NGO
- Government agency
- Zoo/Sanctuary

Technology/Engineering Partners
- Data scientist
- Hardware engineer
- Generalist/hobbyist
- Program manager

In what context do you work with these groups to implement conservation technologies?

	Select the contexts of each collaboration			
	Use	Testing	Adaptation	Development
» Field-based/local conservation group	☐	☐	☐	☐
» International conservation NGO	☐	☐	☐	☐
» Government agency	☐	☐	☐	☐
» Zoo/Sanctuary	☐	☐	☐	☐
» Data scientist	☐	☐	☐	☐
» Hardware engineer	☐	☐	☐	☐
» Generalist/hobbyist	☐	☐	☐	☐
» Program manager	☐	☐	☐	☐
» Software engineer	☐	☐	☐	☐
» Websites, forums, or online tutorials	☐	☐	☐	☐
» Academia - Conservation, Ecology, Biology	☐	☐	☐	☐
» Academia - Engineering	☐	☐	☐	☐
» Academia - Data science	☐	☐	☐	☐
» Collaborative research partnership/Institute	☐	☐	☐	☐
» No one	☐	☐	☐	☐
» Other	☐	☐	☐	☐

Non-Dev Questions

Did you experience any limitations that prevented you from taking part in conservation technology projects? Select all that apply.

- ☐ Cost
- ☐ Timeline
- ☐ Project management
- ☐ Lack of understanding on deliverables
- ☐ Lack of technical support
- ☐ Misunderstanding between scientist and technologist

☐ Lack of partners
☐ None
☐ ____ Other

How interested would you be to participate in the development, adaptation, or testing of new conservation technologies in the future?

○ Never
○ Not very interested
○ Neutral
○ Somewhat Interested
○ Very interested

Dev Questions

The following questions will ask specifically about your experience developing, adapting, and/or testing technologies for conservation applications. For this section, only refer to your most recent experience.

What type of technology did you worked with? Select only one.

Sensors/Hardware
- Camera traps
- Acoustic sensors
- Tracking tags/collars
- Solar power source equipment
- Cell phone
- Handheld GPS
- UAVs/Drones
- Digital/DSLR cameras
- Seismic sensors

How important are the following features for this technology?
Drag and drop to rank. Add non-applicable features to the N/A Group

Items	Ranking Group
Durability	
Ease of Use	
Price	
Power efficiency/battery life	
Data management	N/A Group
Interoperability with other tools/systems	
Connectivity/Real-time transmission	
Other ____	

What limitations (if any) did you experience during the process? Select all that apply.

- ☐ High cost
- ☐ Delayed timeline
- ☐ Lack of project management
- ☐ Misunderstanding on deliverables
- ☐ Lack of technical support
- ☐ Misunderstanding between scientist and technologist
- ☐ Lack of partners
- ☐ No limitations
- ☐ Other

How would you evaluate the experience?

- ○ Very Poor
- ○ Poor
- ○ Acceptable
- ○ Good
- ○ Very Good