Conservation Biology

Contributed Paper

Spatiotemporal trends of illegal activities from ranger-collected data in a Ugandan national park

R. Critchlow,* ¶ A.J. Plumptre,† M. Driciru,‡ A. Rwetsiba,‡ E.J. Stokes,§ C. Tumwesigye,‡ F. Wanyama,‡ and C.M. Beale*

*Department of Biology, University of York, Wentworth Way, Y010 5DD, United Kingdom
†Wildlife Conservation Society, Plot 802 Kiwafu Rd, Kansanga, P.O. Box 7487, Kampala, Uganda
‡Uganda Wildlife Authority, P.O. Box 3530, Kampala, Uganda
§Wildlife Conservation Society, Global Conservation, 2300 Southern Boulevard, Bronx, NY 10460, U.S.A.

Abstract: *Within protected areas, biodiversity loss is often a consequence of illegal resource use. Understanding the patterns and extent of illegal activities is therefore essential for effective law enforcement and prevention of biodiversity declines. We used extensive data, commonly collected by ranger patrols in many protected areas, and Bayesian hierarchical models to identify drivers, trends, and distribution of multiple illegal activities within the Queen Elizabeth Conservation Area (QECA), Uganda. Encroachment (e.g., by pastoralists with cattle) and poaching of noncommercial animals (e.g., snaring bushmeat) were the most prevalent illegal activities within the QECA. Illegal activities occurred in different areas of the QECA. Poaching of noncommercial animals was most widely distributed within the national park. Overall, ecological covariates, although significant, were not useful predictors for occurrence of illegal activities. Instead, the location of illegal activities in previous years was more important. There were significant increases in encroachment and noncommercial plant harvesting (nontimber products) during the study period (1999–2012). We also found significant spatiotemporal variation in the occurrence of all activities. Our results show the need to explicitly model ranger patrol effort to reduce biases from existing uncorrected or capture per unit effort analyses. Prioritization of ranger patrol strategies is needed to target illegal activities; these strategies are determined by protected area managers, and therefore changes at a site-level can be implemented quickly. These strategies should also be informed by the location of past occurrences of illegal activity: the most useful predictor of future events. However, because spatial and temporal changes in illegal activities occurred, regular patrols throughout the protected area, even in areas of low occurrence, are also required.*

Keywords: conservation management, endangered species, Markov chain Monte Carlo (MCMC), ranger-based monitoring, rule breaking, spatial analysis

Tendencias Espacio-Temporales de las Actividades Ilegales a partir de Datos Recolectados por Guardabosques en un Parque Nacional de Uganda

Resumen: *Dentro de las áreas protegidas, la pérdida de la biodiversidad es comúnmente una consecuencia del uso ilegal de los recursos. Por esto, entender los patrones y la extensión de las actividades ilegales es esencial para la aplicación efectiva de la ley y para la prevención de la declinación de la biodiversidad. Usamos datos extensivos, recolectados en su mayoría por patrullas de guardabosques en muchas delas áreas protegidas, y modelos de jerarquía bayesiana para identificar a los conductores, las tendencias y la distribución de múltiples actividades ilegales dentro del Área de Conservación Reina Isabel (ACRI), Uganda. La intrusión (p. ej.: por pastores con ganado) y la caza furtiva de animales no comerciales (p. ej.: la captura por la carne de animales silvestres) fueron las actividades ilegales más prominentes en las diferentes áreas del ACRI. La caza furtiva de animales no comerciales se distribuyó con mayor amplitud dentro del parque nacional. En general, las covariantes ecológicas, aunque significantes, no fueron pronosticadores útiles para la aparición de las actividades ilegales; en su lugar, la ubicación de las actividades ilegales en los años previos fue más importante. Hubo incrementos significativos en la intrusión y la cosecha no comercial*

¶*email rob.critchlow@york.ac.uk*
Paper submitted October 8, 2014; revised manuscript accepted March 1, 2015.

DOI: 10.1111/cobi.12538

de plantas (productos no maderables) durante el periodo de estudio (1999-2012). También encontramos variaciones espacio-temporales en la aparición de todas las actividades. Nuestros resultados muestran la necesidad de modelar explícitamente el esfuerzo de patrullaje de los guardabosques para reducir los sesgos de los análisis existentes de captura por unidad o los que no tienen correcciones. Se necesita de la priorización de las estrategias de patrullaje de los guardabosques para atacar a las actividades ilegales; estas estrategias son determinadas por los administradores de las áreas protegidas y por eso los cambios a nivel de sitio pueden implementarse rápidamente. Estas estrategias también deben informarse con la ubicación de las apariciones pasadas de la actividad ilegal: el pronosticador más útil de eventos futuros. Sin embargo, también se requiere de patrullaje regular en toda el área protegida, incluso en zonas de aparición baja, ya que ocurrieron cambios espaciales y temporales en la actividad ilegal.

Palabras Clave: análisis espacial, cadena de Markov Monte Carlo (MCMC), especies en peligro, infracción de las reglas, manejo de la conservación, monitoreo con base en los guardabosques

Introduction

Global biodiversity is in decline and drivers of these declines, such as, climate change and illegal resource extraction, are increasing (Butchart et al. 2010; Craigie et al. 2010; Laurance et al. 2012). There has been significant loss of habitat throughout the tropics (Achard et al. 2002), where biodiversity is the highest (Hillebrand 2004; Adams & Hadly 2012) and human pressures are growing fastest (Cincotta et al. 2000; Laurance et al. 2012). The decline of tropical biodiversity, even in protected areas (Craigie et al. 2010; Laurance et al. 2012), is often linked to increased illegal harvesting of plants and animals (Butchart et al. 2010; Burn et al. 2011; Maisels et al. 2013). Within protected areas, inefficient law enforcement can result in biodiversity loss (Hilborn et al. 2006; Laurance et al. 2012), whereas effective law enforcement can be a crucial aspect of successful long-term biodiversity conservation (Keane et al. 2008; Craigie et al. 2010; Tranquilli et al. 2012). However, the drivers and spatiotemporal variation of illegal activities within protected areas are poorly understood (Becker et al. 2013; Lindsey et al. 2013). Determining the drivers and patterns of illegal activities would enable more effective law enforcement and potentially reduce the decline of biodiversity within protected areas.

Although it is the rapid rise in poaching of wildlife for the harvesting of high-value products, such as, ivory and rhinoceros horn for international markets that has recently made headline news (Cressey 2013), illegal activities within protected areas include a number of different activities, from encroachment by people for grazing and cultivation, to illegal plant harvesting (including timber extraction and collection of medicinal herbs, thatching grass, etc.), to animal snaring for bushmeat products (Mackenzie & Hartter 2013; Schulte-Herbrüggen et al. 2013). Pressures from illegal activities can be extraordinarily high. Estimates suggest that nearly 10% of the Serengeti wildebeest population is poached each year (Rentsch & Packer 2015), whereas bushmeat hunting in the Serengeti during the 1970s reduced large ungulate populations by 90% (Dublin et al. 1990; Ogutu et al. 2009). Similarly, the area of land illegally logged in protected areas of Kalimantan has been estimated at almost 10% per year between 1999 and 2002 (Curran et al. 2004). The ecosystem consequences of illegal activities within protected areas can be profound (see Beale et al. 2013*b* for a brief review) and range from ecological cascades due to loss of keystone species to total habitat loss due to illegal land conversion. Furthermore, because natural resources are increasingly and unsustainably exploited in regions neighboring unprotected areas, pressures are rising within (Newmark 2008; Wittemyer et al. 2008).

Previous research on illegal resource-use mainly focused on single activities, such as, hunting for bushmeat (Nuno et al. 2013; Watson et al. 2013), illegal logging (Green et al. 2013; Mackenzie & Hartter 2013), or harvesting of rare or medicinal plants (Young et al. 2011). These studies are useful because they provide information about the magnitudes and primary spatial trends in a number of activities. For example, encroachment for grazing appears to be a major threat to protected areas in Kenya (Kiringe et al. 2007), and the demonstration that buffalo (*Syncerus caffer*) populations were lower in locations close to certain villages enabled more effective targeting of ranger patrols (Metzger et al. 2010). However, most studies do not consider the full range of illegal activities that occur within a protected area and assess either temporal or spatial variation alone (but see Mackenzie et al. 2011 and Plumptre et al. 2014). Single activity assessments ignore the potential for different processes to underlie different activities, yet managers need to know the temporal and spatial dynamics of all classes of illegal activity if they are to make informed decisions on resource allocation.

Existing methods to assess patterns of illegal activities from ranger-based monitoring include analysis of raw patterns uncorrected for ranger effort or use of encounter rates per unit effort (e.g., Hilborn et al. 2006; Jachmann 2008*a*; Mackenzie et al. 2011). However, these simple methods can give highly biased results because they are based on the assumption that survey effort is random or uniform across a protected area, yet ranger-based monitoring focuses on areas where illegal activities are expected to be the highest (and are likely to have direct impacts on future events) or are affected by factors such as distance to ranger base and patrol type (Plumptre et al. 2014). Consequently, encounter rates do not reflect the underlying trends of illegal resource-use if the efficiency of ranger patrols improves over time. Depending on the particular assumptions made, these biases may lead to systematic over- or underestimates of illegal activities and will always lead to uncertain trends (Keane et al. 2011). Recently, methods have been developed that can account for spatial and temporal variation in surveillance effort through the estimates of the probability of detecting an event independently from the processes that drive the distribution of the events (Beale et al. 2013*b*, 2014), but these hierarchical models have not yet been applied to ranger-based monitoring data.

We used Bayesian, spatially explicit occupancy models to assess the spatial and temporal patterns in occurrence of 6 classes of illegal activities within the Queen Elizabeth Conservation Area (QECA), Uganda between 1999 and 2012: commercial hunting of high-value mammals, hunting of other animals for bushmeat, encroachment by pastoralists with cattle, subsistence harvesting of plants, and commercial plant harvest (e.g., timber extraction). This data set, derived from ranger patrol data collated using the Management Information System (MIST) database (Stokes 2010), is similar to the data gathered by rangers across many tropical protected areas. Because an understanding of poacher behavior could be very useful for management of protected areas, we aimed to identify areas at greatest risk for each class of illegal activity, identify the ecological and anthropogenic drivers of spatial and temporal variation in illegal activities, and assess the spatial and temporal changes of each activity.

Methods

Our data set consisted of 84,308 position records from 5,867 ranger patrols conducted between September 1999 and October 2012 in QECA, a mixed forest and savannah grassland protected area in southwestern Uganda (Fig. 1). During all surveillance patrols (foot and vehicle), rangers record their location with handheld GPS units when sighting animals or evidence of illegal activities or at 30-min intervals after the last sighting or recorded position. Additional details on the data set are in Supporting Information. Each illegal activity was then assigned to 1 of the 6 classes (encroachment, fishing, plant collection commercial, plant noncommercial, animal poaching commercial, animal noncommercial; Table 1 & Supporting Information) and aggregated annually to a 500 m grid of presence or pseudo-absence. We fitted separate models to each class of activity across the entire period and for annual subsets.

Estimating Ranger Effort

Because locations are recorded by rangers up to 30 min apart, we could not know the exact route of all patrols. Consequently, we estimated the patrol effort between known points based on biased random bridges (Papworth et al. 2012). We used R packages adehabitatLT and adehabitatHR (Calenge 2006) to estimate probable routes between fixed points as a utilization distribution (UD) of each patrol on a 500 m grid. Individual UD surfaces were summed by year to generate annual estimates of observer effort. Fully documented code is available in Supporting Information.

Covariates of Illegal Activity Occurrence

We expected the spatial pattern of illegal activities to be influenced by the following environmental covariates: net primary productivity (NPP), topographic wetness, distances to roads and rivers, terrain slope, wildlife density (target animal density was the density of commercial animal species or combined density of other mammal species targeted by either commercial or noncommercial poachers respectively), and land cover (Supporting Information). Additional details on covariate data are in Supporting Information. Using the digital sources identified in Supporting Information, each of these variables was extracted at 500-m resolution grid in R (R Core Team 2012); finer-scale data were aggregated using the mean value. We included NPP as a proxy for the distribution of wildlife (Loarie et al. 2009; Duffy & Pettorelli 2012) and suitability for illegal grazing (Pettorelli et al. 2009). Areas of high wetness and areas in close proximity to water are also likely to predict areas with relatively high densities of animals (Redfern et al. 2003; Becker et al. 2013), and we assumed these trends were static over the year. We expected evidence of illegal activities to occur closer to roads because roads improve access for human exploitation of natural resources, such as, bushmeat, minerals, and timber (Wato et al. 2006; Laurance et al. 2009; Watson et al. 2013). In addition, land-cover variation will influence animal density and travel cost; illegal activity is more probable closer to human habitation and more detectable in areas of open savannah (Hofer et al. 2000; Plumptre et al. 2014).

Statistical Analyses

We used a Bayesian hierarchical modeling approach to analyze the spatiotemporal distribution of each illegal activity separately. The models had 3 components: a process model defining the relationship between covariates and illegal activities, a component to account for spatial autocorrelation, and a model to explicitly account for temporal and spatial variation in the detection of illegal activities by ranger patrols. Covariates were

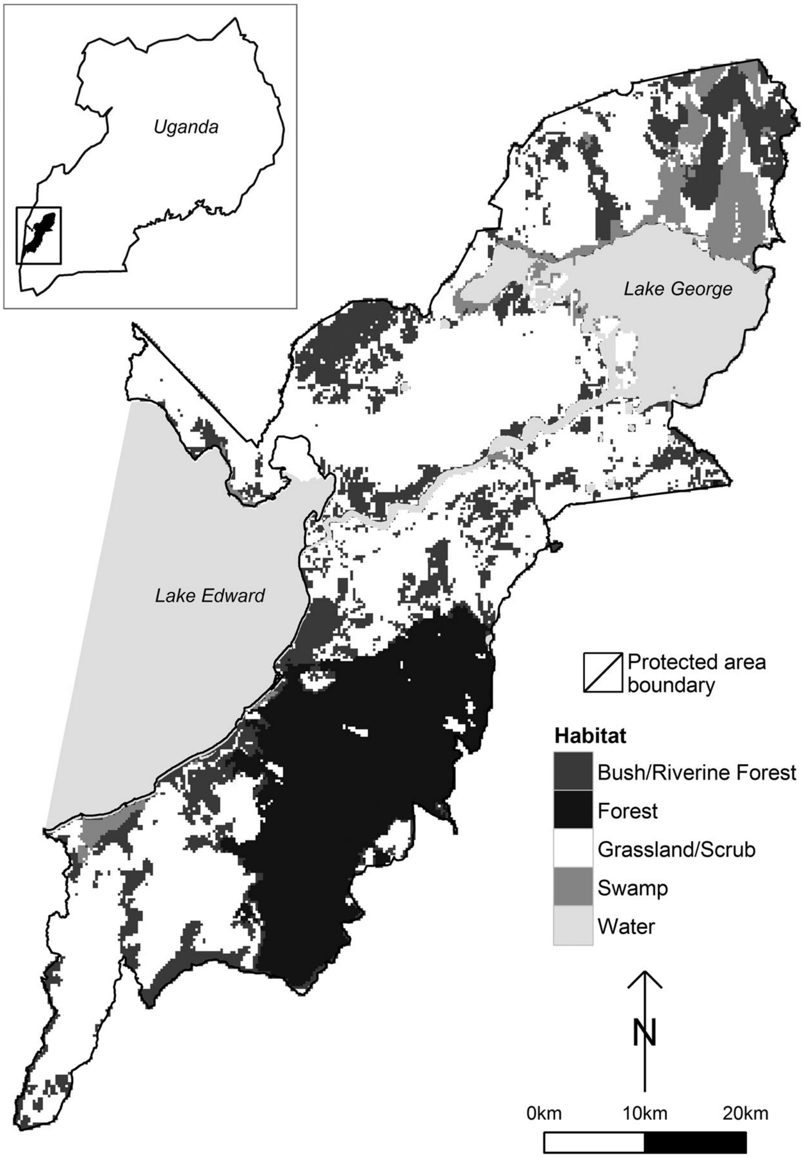

Figure 1. Location of Queen Elizabeth Conservation Area and the broad land cover classifications derived from aerial photographs and high-resolution satellite imagery (Plumptre et al. 2014).

Table 1. Classification of illegal activities within the Queen Elizabeth Conservation Area and associated median probability trends (occurrence) based on data collected from 1999 to 2012.

Activity class	*Examples in MIST[a] database*	*Number of records*	*Occurrence trend (coefficient)*	*Credible intervals (2.5%, 97.5%)*
Encroachment	livestock grazing, mining, trespassing	1570	0.10[b]	0.05, 0.14
Fishing	fishing	443	0.06	−0.04, 0.14
Plant collection commercial	pit sawing, cultivation	260	−0.02	−0.23, 0.10
Plant noncommercial	medicinal plants, grass harvesting	605	0.12[b]	0.06, 0.17
Animal poaching[c] commercial	hippo, elephant, buffalo	241	−0.02	−0.13, 0.06
Animal noncommercial	subsistence hunting, honey harvesting	1589	−0.02	−0.06, 0.03

[a] *Management Information System (Ecological Software Solutions LLC 2009).*
[b] *Significant trend.*
[c] *Although we separate animal poaching into 2 classes, the primary distinction is in the value of the target: commercial poaching involved high-value products from large herbivores, typically procured via active hunting methods, where the product is likely to be transported regionally, whereas noncommercial poaching focused on lower value bushmeat for subsistence or local markets only, typically procured via snares.*

modeled as linear effects, with the exception of NPP and topographic wetness, which were modeled as splines with 2 knots. This model provided an estimate of the true but unknown pattern of illegal activity, independent of the detections of this activity. Full details on the model are provided in Beale et al. (2014) and briefly in the Supporting Information together with R and WinBUGS codes.

Statistical analysis was performed in R (R Core Team 2012), calling WinBUGS (Lunn et al. 2000) through the R2WinBUGS package (Sturtz et al. 2005). We took 1,000 samples from 10,000 Markov chain Monte Carlo (MCMC) iterations after a burn-in of 1,000 iterations.

Our analyses generated separate annual estimates for each activity. To estimate the temporal trends of probabilities of each illegal activity, we needed to look across individual annual models and did so by calculating the mean probability of occurrence across all cells for each year for each of the 1,000 MCMC iterations. Spatiotemporal trends for each activity and each cell were calculated using generalized linear models for each of the 1,000 MCMC iterations with a quasi-binomial error structure (because we were modeling probabilities directly rather than modeling discrete binomial realization of an underlying probability), where the probability of occurrence per cell was the dependent variable and year was the independent variable. Each spatial and temporal model therefore provided 1,000 MCMC estimates of each parameter, which fully propagated model-based uncertainty.

To compare these temporal trends with those resulting from traditional analyses, which either use no correction for effort (raw counts) or use captures per unit effort (CPUE), we used generalized linear models, with a Poisson error structure, for each activity class. For the models of raw counts, ranger effort was the dependent variable and year was the independent variable. For CPUE we used raw counts or effort as the dependent variable and year as the independent variable.

To test whether the covariates we selected were a more accurate predictor of illegal activities than the simple pattern of occurrence of illegal activities over recent years, we calculated the median probability of occurrence (per grid cell) for each year and the probabilities from the previous 5 years with the median annual occurrence probability and effect sizes of all covariates (excluding the random effect).

Results

We successfully fitted 71 of the possible 84 occupancy models (Supporting Information). Models that failed to converge tended to have fewer than 10 recorded events in any year.

Overall Patterns

The spatial distribution of illegal resource use differed among the 6 classes (Fig. 2; corresponding occurrence maps in Supporting Information). Encroachment (mostly illegal cattle grazing in QECA) was the most common at the boundary of the QECA, especially in the northwest, where there was a high population density of cattle in the neighboring land. Commercial plant harvesting (for timber and charcoal) was predicted to be the most likely in a restricted area in southeastern QECA within the Maramagambo Forest. This was also an area where the probability of noncommercial plant harvesting was high. The highest probability of commercial animal poaching was concentrated at lake edges and rivers. In addition, in southern QECA in the Ishasha sector there were areas with a high probability of noncommercial and commercial animal poaching. Relative to the other classes, noncommercial animal poaching was widely distributed across the QECA, and there were few obvious hotspots.

Drivers of Illegal Activities

Parameter values (summarized in Fig. 3; corresponding effect plots in Supporting Information) showed no consistent covariate influenced the probability of all classes of illegal activity, although significant effects (i.e., credible intervals that did not overlap zero) were found for most activities individually, with the exception of encroachment and commercial plant harvesting. Target animal density (i.e., density of commercial animals or combined density of other mammal species that were used for their respective analyses) strongly influenced occurrence of commercial animal poaching (Fig. 3e) but did not influence noncommercial poaching. Land cover also influenced patterns of animal poaching; the probability of all animal poaching was greater in savannah habitats, and noncommercial poaching was the highest in forest habitats. Travel cost from villages did not significantly affect any class of illegal activity, whereas fishing, noncommercial plant harvesting, and noncommercial animal poaching were all higher closer to rivers. For NPP and topographic wetness, there were 2 parameter estimates, representing the knots used in the smooth splines. The pattern of these estimates represented the direction of the effect each variables had on illegal activities. Topographic wetness was never significant, commercial animal poaching was associated with lower levels of NPP, and noncommercial plant harvest and animal poaching were both associated with relatively higher NPP.

Across years and illegal activities (excluding fishing), median cell to cell correlation of the annual occurrence probability with the mean occurrence probability of the previous 5 years was consistently higher than the correlation between the annual occurrence probability and predicted median effect size from covariate models alone

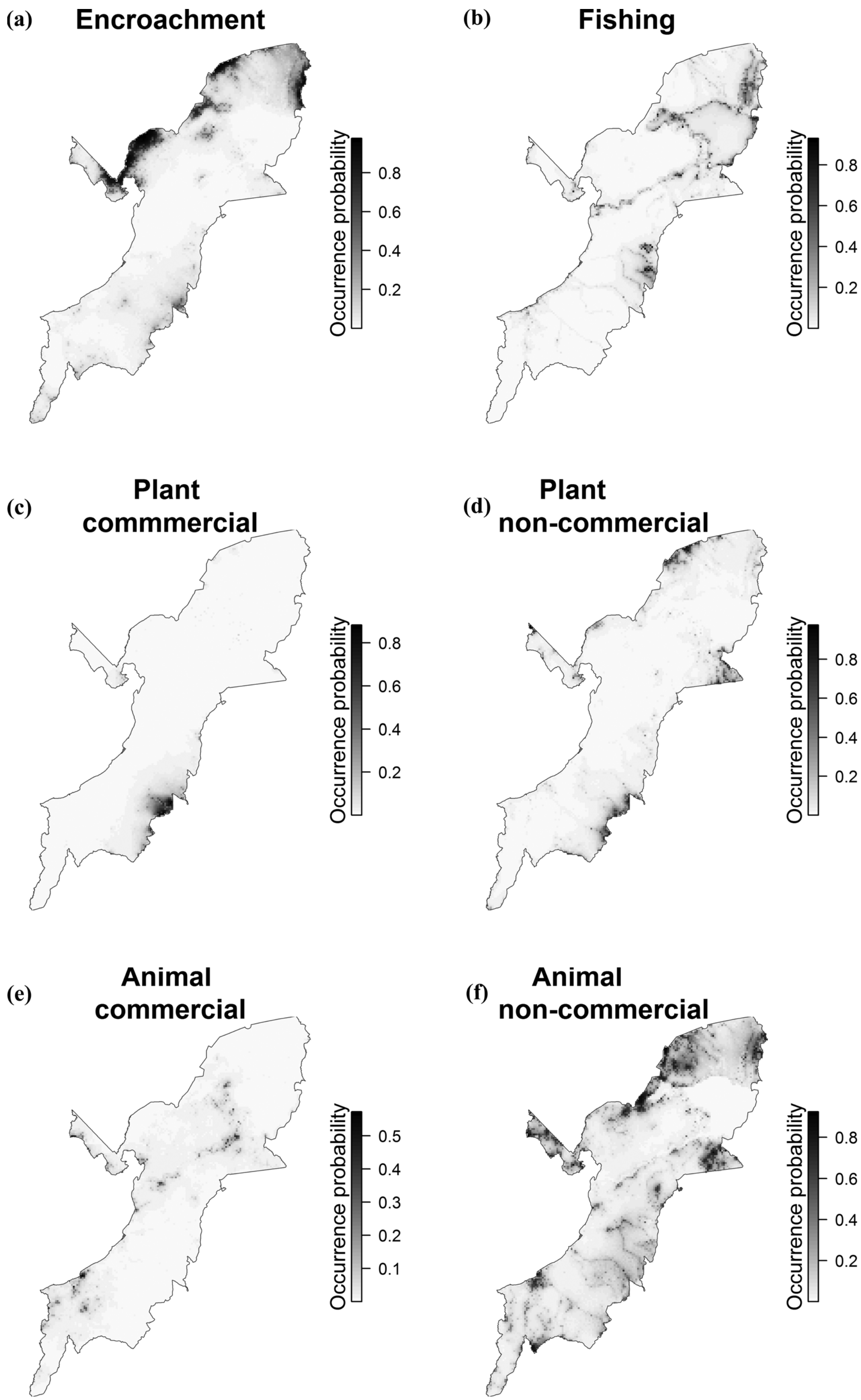

Figure 2. Occurrence probabilities of illegal activities in the Queen Elizabeth Conservation Area: (a) encroachment, (b) fishing, (c) commercial plant harvesting, (d) noncommercial plant harvesting, (e) commercial animal poaching, and (f) noncommercial animal poaching.

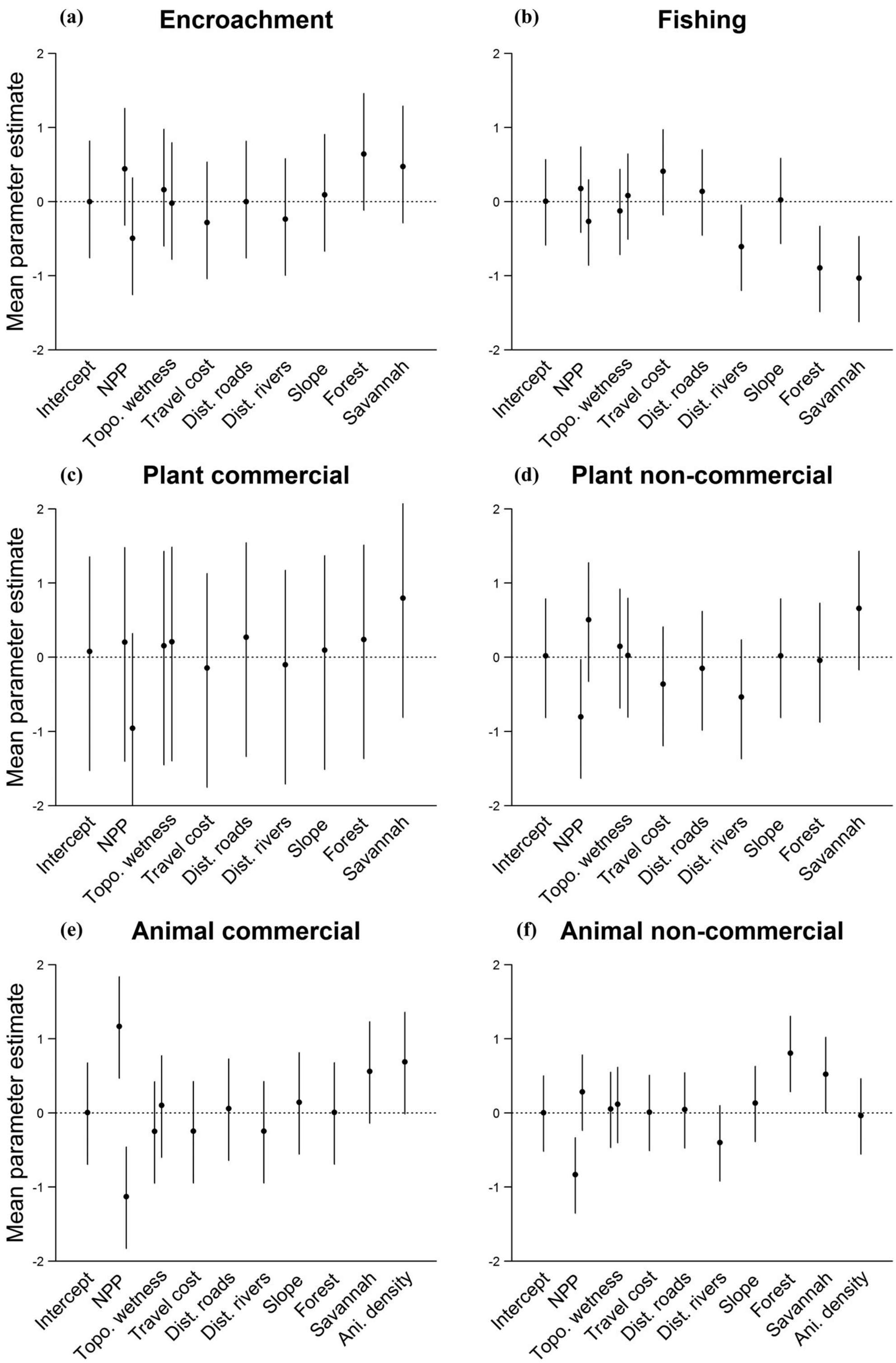

Figure 3. Mean parameter estimates for each covariate (x-axis) across illegal activities occurring in the Queen Elizabeth Conservation Area: (a) encroachment, (b) fishing, (c) commercial plant harvesting, (d) noncommercial plant harvesting, (e) commercial animal poaching, and (f) noncommercial animal poaching. NPP, net primary productivity.

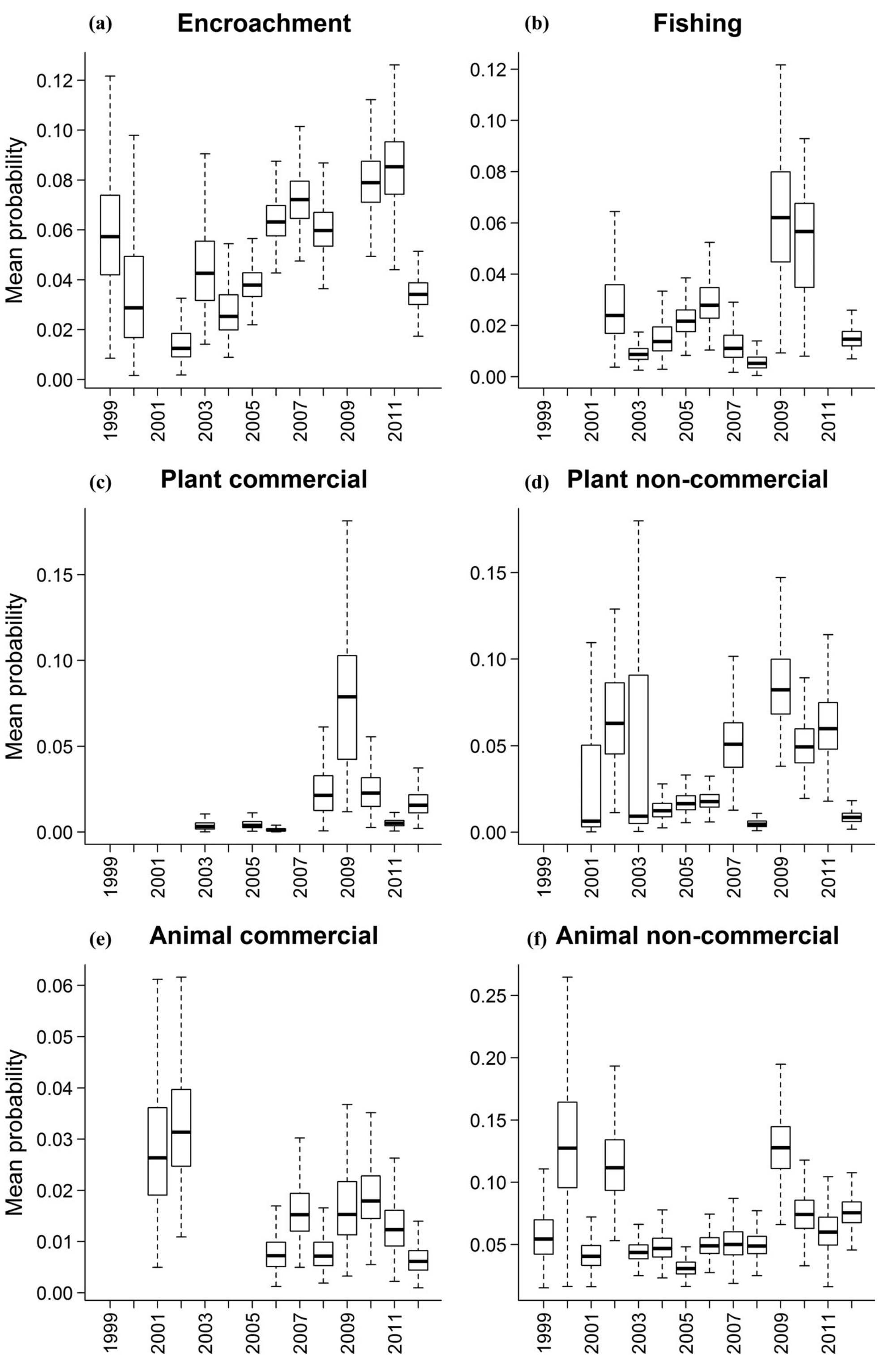

Figure 4. Annual trends in illegal activities in the Queen Elizabeth Conservation Area: (a) encroachment, (b) fishing, (c) commercial plant harvesting, (d) noncommercial plant harvesting, (e) commercial animal poaching, and (f) noncommercial animal poaching. Missing annual data is due to models not converging, which is likely caused by a low number of observations (<10) in that year.

(median difference = 0.17; range = 0.06–0.44; Supporting Information).

Temporal Trends

Across the activities, only encroachment and noncommercial plant harvesting showed significant overall trends (both increasing) between 1999 and 2012 (Table 1), although most activity classes showed a decrease in 2012, and there was often considerable interannual variation (Fig. 4). In contrast, analyses with uncorrected counts suggested increases in all activities (coefficients = 2.06–16.61, $P < 0.01$; Supporting Information), whereas capture per unit effort analyses identified spurious trends in noncommercial animal poaching and commercial plant harvest, negative and positive, respectively (Supporting Information).

Spatiotemporal Trends

Although only 2 activities showed overall temporal trends, we found significant spatiotemporal variation in occurrence of illegal activity for most activity classes (Fig. 5). With the exception of southeastern forest, encroachment increased throughout the QECA (Fig. 5a). Spatiotemporal trends of commercial plant harvest appeared to be driven by roads, rivers, and forest; there was a decrease in activity close to roads and rivers and an increase in activity in densely forested areas.

Commercial animal poaching increased in the most areas, with the exception of central savannah areas and around Lake George in the northern area of the national park. Increase in noncommercial animal poaching between 1999 and 2012 mostly occurred in a few scattered locations and had little apparent pattern.

Discussion

We fitted 71 spatially explicit occupancy models to ranger-derived monitoring data, providing valuable insights into poacher behavior in QECA. We found that the 6 different activities occurred in different areas and correlated with different covariates. Some of these relationships have been identified previously (e.g., commercial animal poaching occurs where animal densities are greatest; Jachmann 2008*b*; Maingi et al. 2012) or are otherwise obvious (e.g., illegal fishing is associated with water), but others are newly identified here (e.g., noncommercial animal poaching was associated with high-wetness areas and near rivers, possibly because there is a need for a certain amount of woody vegetation to conceal snares and create funnels for wildlife to move into the snare). Differences between the estimates of temporal trends among our results and equivalent uncorrected analyses or captures per unit effort (Supporting Information), demonstrate the importance of our independent estimate of the observation process and highlight the unpredictability of the biases in the simpler analyses. In the relatively few examples where we failed to fit a model (13 of 84), there were usually very few detections of the activity in question (<10 per year). This suggests our methods will be widely applicable to similar data sets, provided effort is known and detections are reasonably frequent. Although few activities showed significant overall temporal trends, we found evidence that the spatial occurrence of several activities changed over time (Fig. 5). This information is important to ranger deployment and demonstrates the value of a full spatiotemporal analysis.

Of the 2 classes of illegal activity that increased significantly, encroachment represents perhaps the most immediate threat to the ecological integrity of the QECA (the increase in noncommercial plant harvesting was caused by increased unlicensed harvesting of grass for thatch). The increased incidence of encroachment (Fig. 4) is likely due to the settlement within the QECA of refugees and their 10,000–20,000 cattle from the Democratic Republic of Congo in 2006, their subsequent eviction in 2007, and continued encroachment since then (Moghari 2009). Human density outside the QECA is high (Uganda Bureau of Statistics 2006) close to areas where commercial and noncommercial plant harvesting was most likely. Similar results have been reported in other tropical protected areas, where forest disturbance was more likely closer to higher human density (Allnutt et al. 2013; Mackenzie & Hartter 2013), suggesting that these patterns are primarily driven by the need for fuel and construction (Naughton-Treves et al. 2007; Mackenzie et al. 2011). Covariates for both human and livestock densities were not included in this analysis due to the homogenous data available in this area (e.g., modeled data from the Gridded Livestock of the World; Robinson et al. 2014). In addition, indicators of demand for products (e.g., market prices) were excluded from the analysis because these were available only at regional scales.

Animal poaching is the primary concern of rangers, yet despite investment in antipoaching efforts, we found no overall temporal trend between 1999 and 2012 in either commercial or noncommercial animal poaching. This lack of change should be considered within the context of continentwide increases in demand for bushmeat (Lindsey et al. 2013; Schulte-Herbrüggen et al. 2013) and recent rises in poaching for ivory (Burn et al. 2011; Maisels et al. 2013), factors that suggest current patrol effort is successfully buffering QECA from external drivers. This result is encouraging and demonstrates that traditional law enforcement activities continue to be effective at protecting local sites and preventing increases in poaching, despite global trends. This observation is consistent with data from South Luangwa National Park (Becker et al. 2013) that showed no change in snaring during 2006–2010 and results from southern Africa where despite rises in rhino poaching, other illegal activities remain rare within highly patrolled environments (Beale et al. 2013*a*). Spatially, commercial poaching was primarily associated with a relatively high density of target animals, but there was no equivalent relationship for noncommercial poaching, which was instead more generally dispersed across QECA than other activities. The association of high-value commercial poaching with high density of target animals is unsurprising and confirms earlier results from Maingi et al. (2012). The difference perhaps reflects the differences in absolute abundance of the animal targets of commercial and noncommercial poachers. Commercial poachers must

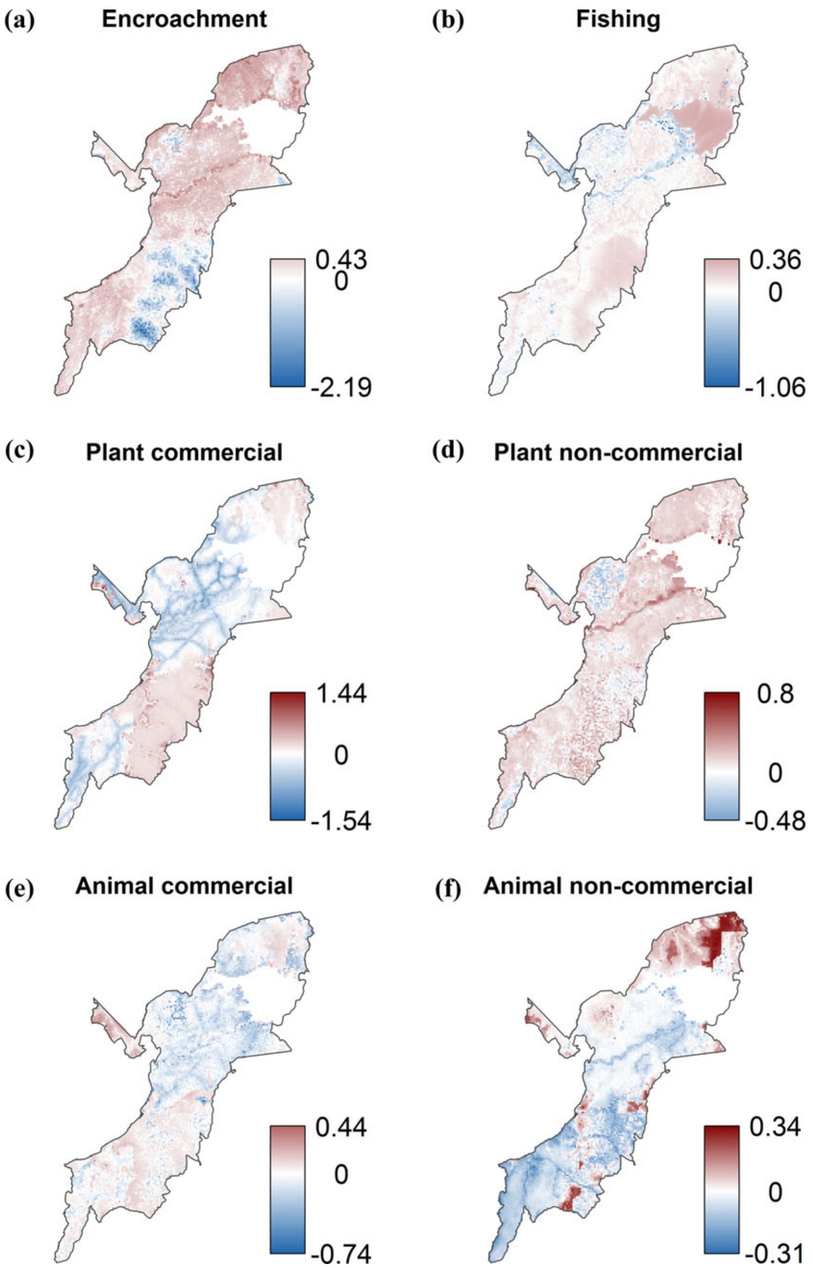

Figure 5. Spatiotemporal trends of illegal activity per grid cell (500 m) between 1999 and 2012 in the Queen Elizabeth Conservation Area: (a) encroachment, (b) fishing, (c) commercial plant harvesting, (d) noncommercial plant harvesting, (e) commercial animal poaching, and (f) noncommercial animal poaching (white, no change; the darker the tone the more significant the trend over the entire period).

hunt relatively few target animals in the areas where they are most abundant, whereas noncommercial poachers may trap sufficient animals in the most convenient areas with little regard to overall density because they are able to leave their snares for several days or weeks.

Although we identified significant correlates for most illegal activity classes, the correlations were generally weak and had wide credible intervals, and we identified none at all for encroachment and noncommercial plant harvesting (Fig. 3, Supporting Information). Several expected patterns were not found. For example, in contrast to studies in Kenya (Wato et al. 2015; Kimanzi et al. 2015) and Bwindi Impenetrable National Park (Twinamatsiko et al. 2014), we found no association between noncommercial animal poaching and travel cost or distance to roads, presumably reflecting differences in poacher behavior between the 2 areas. Instead, much of the spatial pattern was explained by the spatially explicit random effect rather than covariates. There are several possible explanations for this: we missed important covariates, the covariate surfaces we used were not sufficiently accurate, there were strong unmodeled interactions between covariates, or illegal activities were genuinely not strongly correlated with covariates. We consider the first and second possible explanations relatively unlikely because we used a suite of covariates common to similar analyses (e.g., Wato et al. 2006; Watson et al. 2013), we did find evidence of significant effects with most covariates, and we have considerable first-hand experience of QECA that confirms the reliability of the surfaces used. There are perhaps good reasons to expect complex interactions between covariates. Travel cost may be weighed up against animal density or individuals may be seeking to optimize their success at multiple activities at once. An illegal pastoralists with cattle may well seek to set snares while in the protected area but may be unlikely to do so in the immediate vicinity of their own cattle. Such interactions may be real but are too complex to estimate given the noisy data available, meaning that for practical purposes this explanation and the final one are equivalent: illegal activities in QECA were not strongly correlated with simple environmental covariates. Although this does mean it is difficult to predict patterns of illegal activity based on covariates alone, and despite significant spatiotemporal variation over the long term, our annual models showed broadly similar patterns for each activity year after year. Encroachment tended to occur in the northwest, illegal logging in the Maramagambo forest, commercial animal poaching along the Kazinga channel, etc. Consequently, the best empirical prediction of future poaching activity will come from the current distribution, and intelligence-driven ranger patrols based on the detailed knowledge generated through these analyses will likely improve detections of illegal activities.

Although the past does seem to be the best predictor of the future for the illegal activities we analyzed, our spatiotemporal analysis provides evidence that longer term changes in illegal activities occur, revealing relatively subtle changes in illegal activities that may be missed by spatial or temporal analyses alone. These changes presumably reflect changes in poacher behavior either in response to changing ranger effort (e.g., the decrease in commercial animal poaching in the south may be associated with the large increase in ranger effort in this region over the study period) or as a consequence of changing demand for different natural products (e.g., the decline in plant harvesting along rivers [Fig. 5c] probably reflects declines in demand for fishing floats from *Aeschynomene elaphroxylon* [Ambatch] trees as a consequence of legal supply being made available elsewhere [A.J. Plumptre, personal observation]). Such temporal change in poacher behavior is often suggested (Keane et al. 2008) and forms the justification of a deterrence-based approach to ranger activities, but these results provide strong empirical support for such temporal behavioral shifts. A consequence of this is that although optimizing ranger effort in high-occurrence areas is generally wise, it remains important to maintain sufficient patrol effort in areas where detections are expected to be lower to monitor spatial change in patterns over time, a similar recommendation to that of Watson et al. (2013). Determining the deterrence effects of patrols and identifying the threshold at which patrol effort prevents the occurrence of illegal activities are important future requirements and will aid patrol strategy decisions and improve patrol efficiency in resource-limited settings.

Acknowledgments

This work was funded by the USAID CAFEC program, the Moore Foundation, and the Wildlife Conservation Society. We are grateful to the Uganda Wildlife Authority for sharing their ranger-collected data from Queen Elizabeth National Park and contributing inputs to the interpretation of the analyses. We are also grateful to all the rangers and wardens who have been involved in collecting these data and working to protect the biodiversity of this park.

Supporting Information

Additional details describing the database and on obtaining covariate data and statistical analysis (Appendix S1), R code for the effort calculation and covariate manipulations (Appendix S2), WinBUGS code (Appendix S3), a list of illegal activities as reported in the MIST database (Appendix S4), details on ecological covariates (Appendix S5), model completion success (Appendix S6), location maps of illegal activities (Appendix S7), correlation between annual probabilities and the probabilities of the previous 5 years (Appendix S8),temporal trends of raw counts of illegal activities and CPUE (Appendix S9), comparison of trend analyses (Appendix S10), correlation of covariates (Appendix S11), marginal effects for all 6 illegal activity classes (Appendices S12–S17), and the relationship between ranger effort and detectability (Appendix S18) are available as part of the on-line article. The authors are solely responsible for the content and functionality of these materials. Queries (other than absence of material) should be directed to the corresponding author.

Literature Cited

Achard F, Eva HD, Stibig H-J, Mayaux P, Gallego J, Richards T, Malingreau J-P. 2002. Determination of deforestation rates of the world's humid tropical forests. Science **297:**999–1002.

Adams RI, Hadly EA. 2012. Genetic diversity within vertebrate species is greater at lower latitudes. Evolutionary Ecology **27:**133–143.

Allnutt TF, Asner GP, Golden CD, Powell GVN. 2013. Mapping recent deforestation and forest disturbance in northeastern Madagascar. Tropical Conservation Science **6:**1–15.

Beale CM, et al. 2013*a*. Ten lessons for the conservation of African savannah ecosystems. Biological Conservation **167:**224–232.

Beale CM, Baker NE, Brewer MJ, Lennon JJ. 2013*b*. Protected area networks and savannah bird biodiversity in the face of climate change and land degradation. Ecology Letters **16:**1061–1068.

Beale CM, Brewer MJ, Lennon JJ. 2014. A new statistical framework for the quantification of covariate associations with species distributions. Methods in Ecology and Evolution **5:**421–432.

Becker M, McRobb R, Watson F, Droge E, Kanyembo B, Murdoch J, Kakumbi C. 2013. Evaluating wire-snare poaching trends and the impacts of by-catch on elephants and large carnivores. Biological Conservation **158:**26–36.

Burn RW, Underwood FM, Blanc J. 2011. Global trends and factors associated with the illegal killing of elephants: a hierarchical Bayesian analysis of carcass encounter data. PLOS ONE **6**(e24165) DOI: 10.1371/journal.pone.0024165.

Butchart SHM, et al. 2010. Global biodiversity: indicators of recent declines. Science **328:**1164–1168.

Calenge C. 2006. The package adehabitat for the R software: tool for the analysis of space and habitat use by animals. Ecological Modelling **197:**516–519.

Cincotta RP, Wisnewski J, Engelman R. 2000. Human population in the biodiversity hotspots. Nature **404:**990–992.

Craigie ID, Baillie JEM, Balmford A, Carbone C, Collen B, Green RE, Hutton JM. 2010. Large mammal population declines in Africa's protected areas. Biological Conservation **143:**2221–2228.

Cressey D. 2013. Nations fight back on ivory. Nature **503:**452.

Curran LM, Trigg SN, McDonald AK, Astiani D, Hardiono YM, Siregar P, Caniago I, Kasischke E. 2004. Lowland forest loss in protected areas of Indonesian Borneo. Science **303:**1000–1003.

Dublin HT, Sinclair ARE, Boutin S, Anderson E, Jago M, Arcese P. 1990. Further evidence from Serengeti, Tanzania. Oecologia **82:** 283–288.

Duffy JP, Pettorelli N. 2012. Exploring the relationship between NDVI and African elephant population density in protected areas. African Journal of Ecology **50:**455–463.

Ecological Software Solutions LLC. 2009. MIST Version 2.2.3.4. Hegymagas, Hungary.

Green JMH, Larrosa C, Burgess ND, Balmford A, Johnston A, Mbilinyi BP, Platts PJ, Coad L. 2013. Deforestation in an African biodiversity hotspot: extent, variation and the effectiveness of protected areas. Biological Conservation **164:**62–72.

Hilborn R, Arcese P, Borner M, Hando J, Hopcraft G, Loibooki M, Mduma S, Sinclair ARE. 2006. Effective enforcement in a conservation area. Science **314:**1266.

Hillebrand H. 2004. On the generality of the latitudinal diversity gradient. The American Naturalist **163:**192–211.

Hofer H, Campbell KLI, East ML, Huish SA. 2000. Modeling the spatial distribution of the economic costs and benefits of illegal game meat hunting in the Serengeti. Natural Resource Modeling **13:**151–177.

Jachmann H. 2008*a*. Monitoring law-enforcement performance in nine protected areas in Ghana. Biological Conservation **141:**89–99.

Jachmann H. 2008*b*. Illegal wildlife use and protected area management in Ghana. Biological Conservation **141:**1906–1918.

Keane A, Jones JPG, Edwards-Jones G, Milner-Gulland EJ. 2008. The sleeping policeman: understanding issues of enforcement and compliance in conservation. Animal Conservation **11:**75–82.

Keane A, Jones JPG, Milner-Gulland EJ. 2011. Encounter data in resource management and ecology: pitfalls and possibilities. Journal of Applied Ecology **48:**1164–1173.

Kimanzi JK, Sanderson RA, Rushton SP, Mugo MJ. 2015. Spatial distribution of snares in Ruma National Park, Kenya, with implications for management of the roan antelope Hippotragus equinus langheldi and other wildlife. Oryx **49:**295–302.

Kiringe JW, Okello MM, Ekajul SW. 2007. Managers' perceptions of threats to the protected areas of Kenya: prioritization for effective management. Oryx **41:**314–321.

Laurance WF, Goosem M, Laurance SGW. 2009. Impacts of roads and linear clearings on tropical forests. Trends in Ecology & Evolution **24:**659–669.

Laurance WF, et al. 2012. Averting biodiversity collapse in tropical forest protected areas. Nature **489:**290–294.

Lindsey PA, et al. 2013. The bushmeat trade in African savannas: impacts, drivers, and possible solutions. Biological Conservation **160:**80–96.

Loarie SR, vanAarde RJ, Pimm SL. 2009. Elephant seasonal vegetation preferences across dry and wet savannas. Biological Conservation **142:**3099–3107.

Lunn DJ, Thomas A, Best N, Spiegelhalter D. 2000. WinBUGS—a Bayesian modelling framework: concepts, structure, and extensibility. Statistics and Computing **10:**325–337.

Mackenzie CA, Chapman CA, Sengupta R. 2011. Spatial patterns of illegal resource extraction in Kibale National Park, Uganda. Environmental Conservation **39:**38–50.

Mackenzie CA, Hartter J. 2013. Demand and proximity: drivers of illegal forest resource extraction. Oryx **47:**288–297.

Maingi JK, Mukeka JM, Kyale DM, Muasya RM. 2012. Spatiotemporal patterns of elephant poaching in south-eastern Kenya. Wildlife Research **39:**234–239.

Maisels F, et al. 2013. Devastating decline of forest elephants in central Africa. PLOS ONE **8**(e59469) DOI: 10.1371/journal.pone.0059469.

Metzger KL, Sinclair ARE, Hilborn R, Hopcraft JGC, Mduma SAR. 2010. Evaluating the protection of wildlife in parks: the case of African buffalo in Serengeti. Biodiversity and Conservation **19:**3431–3444.

Moghari NM. 2009. A Survey of Queen Elizabeth National Park (QENP) Communities' Attitudes Toward Human-Lion Conflict and Lion Conservation. PhD thesis. George Mason University, Washington, D.C.

Naughton-Treves L, Kammen D, Chapman C. 2007. Burning biodiversity: woody biomass use by commercial and subsistence groups in western Uganda's forests. Biological Conservation **134:**232–241.

Newmark WD. 2008. Isolation of African protected areas. Frontiers in Ecology and the Environment **6:**321–328.

Nuno A, Bunnefeld N, Naiman LC, Milner-Gulland EJ. 2013. A novel approach to assessing the prevalence and drivers of illegal bushmeat hunting in the serengeti. Conservation Biology **27:**1355–1365.

Ogutu JO, Piepho H-P, Dublin HT, Bhola N, Reid RS. 2009. Dynamics of Mara-Serengeti ungulates in relation to land use changes. Journal of Zoology **278:**1–14.

Papworth SK, Bunnefeld N, Slocombe K, Milner-Gulland EJ. 2012. Movement ecology of human resource users: using net squared displacement, biased random bridges and resource utilization functions to quantify hunter and gatherer behaviour. Methods in Ecology and Evolution **3:**584–594.

Pettorelli N, Bro-Jørgensen J, Durant SM, Blackburn T, Carbone C. 2009. Energy availability and density estimates in African ungulates. The American Naturalist **173:**698–704.

Plumptre AJ, Fuller RA, Rwetsiba A, Wanyama F, Kujirakwinja D, Driciru M, Nangendo G, Watson JEM, Possingham HP. 2014. Efficiently targeting resources to deter illegal activities in protected areas. Journal of Applied Ecology **51:**714–725.

R Core Team. 2012. R: A Language and Environment for Statistical Computing. Vienna.

Redfern JV, Grant R, Biggs H, Getz WM. 2003. Surface water contraits on herbivore foraging in the Kruger National Park, South Africa. Ecology **84:**2092–2107.

Rentsch D, Packer C. 2015. The effect of bushmeat consumption on migratory wildlife in the Serengeti ecosystem, Tanzania. Oryx **49:** 287–294.

Robinson TP, Wint GRW, Conchedda G, VanBoeckel TP, Ercoli V, Palamara E, Cinardi G, D'Aietti L, Hay SI, Gilbert M. 2014. Mapping the global distribution of livestock. PLOS ONE **9**(e96084) DOI: 10.1371/journal.pone.0096084.

Schulte-Herbrüggen B, Cowlishaw G, Homewood K, Rowcliffe JM. 2013. The importance of bushmeat in the livelihoods of West African cash-crop farmers living in a faunally-depleted landscape. PLOS ONE **8**(e72807) DOI: 10.1371/journal.pone.0072807.

Stokes EJ. 2010. Improving effectiveness of protection efforts in tiger source sites: Developing a framework for law enforcement monitoring using MIST. Integrative Zoology **5:**363–377.

Sturtz S, Ligges U, Gelman A. 2005. R2WinBUGS: a package for running WinBUGS from R. Journal of Statistical Software **12:**1–16.

Tranquilli S, et al. 2012. Lack of conservation effort rapidly increases African great ape extinction risk. Conservation Letters **5:**48–55.

Twinamatsiko M, Baker J, Harisson M, Shirkhorshidi M, Bitariho R, Wieland M, Asuma S, Milner-Gulland EJ, Franks P, Roe D. 2014. Linking conservation, equity and poverty alleviation understanding profiles and motivations of resource users and local perceptions of governance at Bwindi Impenetrable National Park, Uganda. Research report. IIED, London.

Uganda Bureau of Statistics. 2006. 2002 Uganda population and housing census—Analytical Report—Population Size and Distribution. Uganda Bureau of Statistics, Kampala.

Wato YA, Wahungu GM, Okello MM. 2006. Correlates of wildlife snaring patterns in Tsavo West National Park, Kenya. Biological Conservation **132:**500–509.

Watson F, Becker M, McRobb R, Kanyembo B. 2013. Spatial patterns of wire-snare poaching: Implications for community conservation in buffer zones around National Parks. Biological Conservation **168:**1–9.

Wittemyer G, Elsen P, Bean WT, Burton ACO, Brashares JS. 2008. Accelerated human population growth at protected area edges. Science **321:**123–126.

Young JA, vanManen FT, Thatcher CA. 2011. Geographic profiling to assess the risk of rare plant poaching in natural areas. Environmental Management **48:**577–587.