



Mechanistic understanding of human–wildlife conflict through a novel application of dynamic occupancy models

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Abstract: *Crop and livestock depredation by wildlife is a primary driver of human–wildlife conflict, a problem that threatens the coexistence of people and wildlife globally. Understanding mechanisms that underlie depredation patterns holds the key to mitigating conflicts across time and space. However, most studies do not consider imperfect detection and reporting of conflicts, which may lead to incorrect inference regarding its spatiotemporal drivers. We applied dynamic occupancy models to elephant crop depredation data from India between 2005 and 2011 to estimate crop depredation occurrence and model its underlying dynamics as a function of spatiotemporal covariates while accounting for imperfect detection of conflicts. The probability of detecting conflicts was consistently <1.0 and was negatively influenced by distance to roads and elevation gradient, averaging 0.08–0.56 across primary periods (distinct agricultural seasons within each year). The probability of crop depredation occurrence ranged from 0.29 (SE 0.09) to 0.96 (SE 0.04). The probability that sites raided by elephants in primary period t would not be raided in primary period $t + 1$ varied with elevation gradient in different seasons and was influenced negatively by mean rainfall and village density and positively by distance to forests. Negative effects of rainfall variation and distance to forests best explained variation in the probability that sites not raided by elephants in primary period t would be raided in primary period $t + 1$. With our novel application of occupancy models, we teased apart the spatiotemporal drivers of conflicts from factors that influence how they are observed, thereby allowing more reliable inference on mechanisms underlying observed conflict patterns. We found that factors associated with increased crop accessibility and availability (e.g., distance to forests and rainfall patterns) were key drivers of elephant crop depredation dynamics. Such an understanding is essential for rigorous prediction of future conflicts, a critical requirement for effective conflict management in the context of increasing human–wildlife interactions.*

Keywords: citizen science, crop and livestock depredation, detection probability, elephants, human-dominated landscapes, monitoring, predictive modeling

Entendimiento Mecánico del Conflicto Humano – Animales Silvestre a través de la Novedosa Aplicación de los Modelos Dinámicos de Ocupación

Resumen: *La depredación de cultivos y ganado por parte de animales silvestres es un conductor principal del conflicto humano – animales silvestres, un problema que amenaza la coexistencia de la gente y la vida silvestre a nivel global. Entender los mecanismos que son la base de los patrones de depredación es la clave para mitigar los conflictos a lo largo del tiempo y el espacio. Sin embargo, la mayoría de los estudios no consideran la detección imperfecta y el reporte de conflictos, lo que puede llevar a la interferencia incorrecta*

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con respecto a los conductores espacio-temporales. Aplicamos modelos dinámicos de ocupación a datos de depredación de cultivos por elefantes en India desde 2005 y hasta 2011 para estimar la incidencia de depredación de cultivos y modelar sus dinámicas como una función de covarianzas espacio-temporales mientras representan la detección imperfecta de los conflictos. La probabilidad de detectar conflictos fue constantemente <1.0 y estuvo influenciada negativamente por la distancia a las carreteras y el gradiente de elevación, promediando 0.08 - 0.56 en los periodos primarios (temporadas agrícolas distintas dentro de cada año). La probabilidad de la incidencia de depredación de cultivos varió desde 0.29 (SE 0.09) hasta 0.96 (SE 0.04). La probabilidad de que los sitios saqueados por elefantes en un periodo primario t no fueran saqueados en un periodo primario $t + 1$ varió con el gradiente de elevación en diferentes temporadas y estuvo influenciado negativamente por la precipitación promedio y la densidad de la aldea y positivamente por la distancia a los bosques. Los efectos negativos de la variación en la precipitación y la distancia a los bosques explicaron de mejor manera la variación en la probabilidad de que los sitios no saqueados por elefantes en el periodo primario t serían saqueados en el periodo primario $t + 1$. Con nuestra novedosa aplicación de los modelos de ocupación, separamos a los conductores espacio-temporales de los factores que influyen en cómo son observados, permitiendo así la inferencia más fiable de los mecanismos que son la base de los patrones observados de los conflictos. Encontramos que los factores asociados con el incremento en la disponibilidad y accesibilidad de los cultivos (p. ej.: la distancia a los bosques y los patrones de precipitación) fueron conductores clave en las dinámicas de depredación de cultivos de los elefantes. Tal entendimiento es esencial para una predicción rigurosa de conflictos futuros, un requerimiento crítico para el manejo efectivo de conflictos en el contexto de las crecientes interacción humano - animales silvestres.

Palabras Clave: ciencia ciudadana, depredación de cultivos y ganado, detección de probabilidad, elefantes, modelado predictivo, monitoreo, terrenos dominados por humanos

Introduction

Conflict between people and wildlife—typically involving species that compete with humans for space and resources (Woodroffe et al. 2005)—is a pervasive conservation challenge. Crop or livestock depredation by wildlife imposes substantial costs on local people and their livelihoods (Madhusudan 2003; Karanth et al. 2013). Concurrently, human incursions into wildlife habitat and retributive killing of conflict-prone species threaten the persistence of endangered fauna living in close proximity to people (Woodroffe & Ginsberg 1998; Goswami et al. 2014). Recurrent conflicts not only undermine the well-being of both people and wildlife (Madhusudan 2003), they also encumber local support for conservation (Naughton-Treves et al. 2003). Therefore, the effective management of human–wildlife conflict (HWC) is an essential precondition for the coexistence of wildlife and people across space and over time (Madden 2004).

Crop and livestock depredation is a major source of HWC across the world (Sukumar 2003; Treves & Karanth 2003; Woodroffe et al. 2005). Consequently, a central focus of HWC research has been to investigate the patterns and spatiotemporal correlates of crop and livestock depredation so as to better inform conflict mitigation strategies (e.g., Sitati et al. 2003; Gubbi 2012; Karanth et al. 2013). Data for such studies are typically obtained from local informants, respondents to questionnaires or official records of reported conflicts. Within such a framework, if a depredation event is reported, it is known with certainty that it has occurred (assuming the report is

verified to avoid false positives). However, if a depredation event is not recorded or reported, it could imply either that such an event has not occurred or that it did occur but was not detected or reported. Therefore, the reporting of conflicts is analogous to the detection of animals when attempting to estimate demographic parameters or species occurrence (Williams et al. 2002; MacKenzie et al. 2006).

Biases in conflict reporting probability may arise due to factors such as variable search effort, whereby conflicts from remote or inaccessible locations may be underreported because of lower sampling effort in these areas. Such concerns have recently been raised about citizen science surveys, where imperfect detection or reporting of data generated opportunistically under a participatory research framework can potentially bias estimates of population trends (Kéry et al. 2010; van Strien et al. 2013). Occupancy models are designed to appropriately account for imperfect detection and variable observation efforts (MacKenzie et al. 2006) and can provide reliable estimates of species occurrence in participatory research surveys (Karanth et al. 2009; Kéry et al. 2010). These models could be just as effective and robust in quantifying HWC when conflicts are imperfectly detected or reported.

We used data on conflicts between people and the Asian elephant (*Elephas maximus*) in Garo Hills, India, in a novel application of occupancy modeling to HWC research. Elephants are focal species for HWC research, given the damage they can inflict on human life and livelihoods (Madhusudan 2003) and the detrimental effects of human–elephant conflict (HEC) on elephant

Table 1. Hypotheses and a priori predictions about the influence of spatiotemporal covariates on human–elephant conflict (HEC) detection and reporting probabilities^a ($p_{t,j}$), as well as on the extinction^a (ε_t) and colonization^a (γ_t) of elephant crop depredation events.

Hypothesis	covariate	Covariate effects	
		predicted direction of slope parameter (β) ^a	estimated β (SE) ^b
Detection or reporting of conflict is low in less accessible locations.	distance to roads	$p_{t,j}: -$	$p_{t,j}: -0.63 (0.17 \times 10^{-3})$
	ruggedness index	$p_{t,j}: -$	$p_{t,j}: -0.1 (0.03)$
Elephant crop depredation dynamics are a function of season-specific variation in the spatial location of crops.	season \times ruggedness index (RG)	$\varepsilon_t: -$ for jhum (JHM) \times RG; + for paddy (PD) \times RG and fallow (FL) \times RG	$\varepsilon_{tJHM \times RG}: -3.84 (1.54)$ $\varepsilon_{tPD \times RG}: 0.52 (1.85)$ $\varepsilon_{tPD \times RG}: 2.04(3.4)$
		$\gamma_t: +$ for jhum (JHM) \times RG; $-$ for paddy (PD) \times RG and fallow (FL) \times RG	$\gamma_t: \text{no support for covariate}$
Elephant crop depredation increases with an increase in rainfall, a key determinant of primary productivity in terrestrial ecosystems.	mean rainfall lagged by 2 months ($\bar{R}_{t[-2]}$) coefficient of variation of rainfall lagged by 2 months ($R_{t[-2]}^C$)	$\varepsilon_t: -$	$\varepsilon_t: -0.003 (0.001)$
		$\gamma_t: +$	$\gamma_t: 0.35 \times 10^{-3} (0.29 \times 10^{-3})^c$
		$\varepsilon_t: +$ $\gamma_t: -$	$\varepsilon_t: -10.9 (4.41)^c$ $\gamma_t: -6.04 (3.17)$
Elephant crop depredation increases as accessibility to crop fields increases.	distance to closest forest village density	$\varepsilon_t: +$	$\varepsilon_t: 0.74 \times 10^{-3} (0.57 \times 10^{-3})$
		$\gamma_t: -$	$\gamma_t: -0.33 (0.33 \times 10^{-3})$
		$\varepsilon_t: -$ $\gamma_t: +$	$\varepsilon_t: -2.46 (1.41)$ $\gamma_t: 0.77 (0.98)^c$

^aKey: $p_{t,j}$, probability that at least one HEC event was reported during a single month j of primary period t during which at least one such event occurred; ε_t , probability that sites raided by elephants in primary period t are not raided in primary period $t + 1$; γ_t , probability that sites not raided by elephants in primary period t are raided in primary period $t + 1$.

^bBased on the top model in Supporting Information.

^cBased on the best supported model that included this covariate.

population persistence in areas where they co-occur with people (Goswami et al. 2014). Depredation of cultivated crops by elephants is the primary source of HEC in both Africa and Asia (Sukumar 2003), and rigorous quantitative assessments of its spatiotemporal correlates are essential for the prediction and management of future conflicts. Crop fields potentially represent resource-rich patches because cultivated crops typically have higher nutritional value and water retention capacity relative to forest vegetation and are more palatable (Sukumar 2003; Chiyo et al. 2005). Therefore, depredation patterns may be expected to coincide with spatiotemporal conditions that maximize crop availability and accessibility to elephants (Chiyo et al. 2005; Webber et al. 2011).

We applied multiseason occupancy models (MacKenzie et al. 2003) to more than 6 years of elephant crop depredation data to quantify crop depredation patterns and to discern its potential drivers in a fragmented landscape while accounting for imperfect detection and reporting of conflicts. We tested whether accessibility of sampling sites affected the probability of detection and reporting of conflicts and determined whether probabilities of crop depredation dynamics were driven by factors influencing crop availability and accessibility. Specific hypotheses and a priori predictions are in Table 1. Inferences thus gathered allowed us to map potential conflict

areas and to discuss the implications of our findings for HWC research and the management of conflicts between elephants and people.

Methods

Study Area

Our study area in Garo Hills was a fragmented landscape with a mosaic of community-managed forests and 4 government-managed protected areas (PAs) (Baghmara Reserve Forest, Balphakram National Park, Siju Wildlife Sanctuary, and Rewak Reserve Forest) interspersed in a matrix of agriculture and human habitation (Fig. 1). Dominant agricultural land uses in the matrix included slash-and-burn shifting cultivation (locally known as *jhum*), paddy cultivation, and monoculture cash-crop plantations. Road accessibility within the landscape was largely limited to 2 major roads running in north–south and east–west directions.

Average monthly rainfall in Garo Hills is approximately 1900 mm, and most of it falls from April to September (mean monthly rainfall during this period is approximately 3360 mm) (Indian Institute of Tropical Meteorology, unpublished data). Agricultural

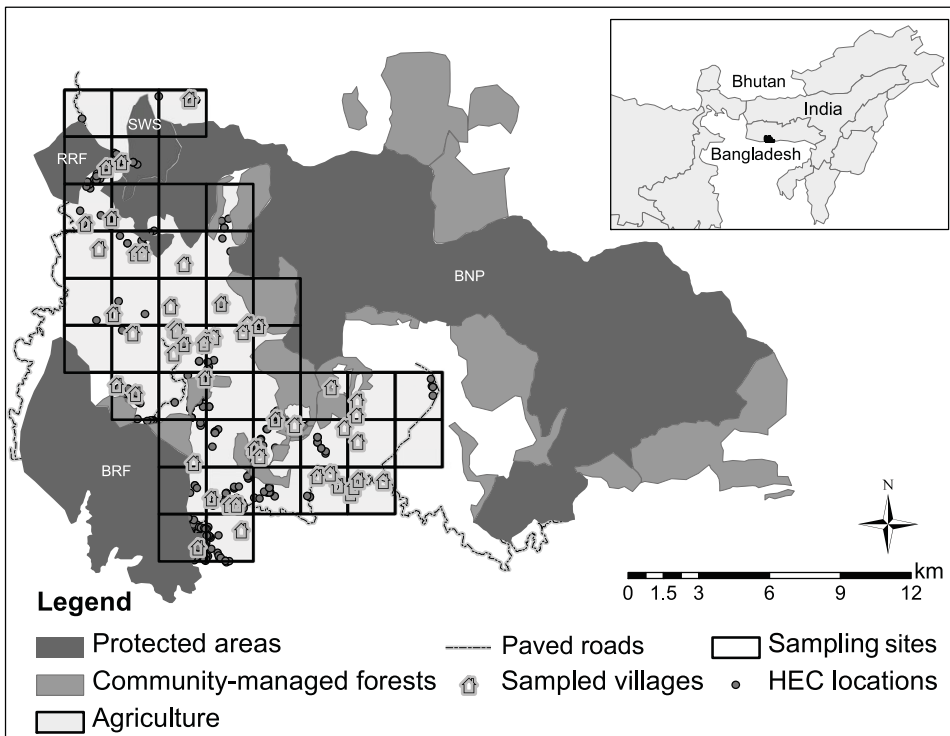


Figure 1. Study area in Garo Hills, India (black polygon in the inset). Protected areas included Baghmara Reserve Forest (BRF), Balphakram National Park (BNP), Siju Wildlife Sanctuary (SWS), and Rewak Reserve Forest (RRF). The agricultural matrix (agriculture) was of slash-and-burn shifting cultivation, paddy cultivation, and monoculture cash-crop plantations. Sampling sites included grid cells of 4 km².

seasons in the region are determined by rainfall patterns and can be broadly classified as fallow season (January–March), jhum season (April–September), and paddy season (July–December). These seasons are defined thoroughly in the section “Analytical Design and Occupancy Modeling.”

Quantification of Conflicts

We adapted methods that were successfully used to quantify HEC in Africa (Sitati et al. 2003) for use in our study area. We trained a team of 17 informants to record and report conflicts from communal lands owned and managed by residents of 49 villages across the study area (Fig. 1). Informants collected data from June 2005 to October 2011. Each informant verified HEC reports from 2 to 3 villages, recorded the locations of these conflicts with a global positioning system (GPS), and collated the information on a standardized data collection form. We visited each informant once a month to monitor the recording of HEC and to retrieve the data collection forms. Crop depredation was the primary form of HEC; reports of property damage and human injury were negligible.

Analytical Design and Occupancy Modeling

An occupancy-modeling framework typically uses binomial or multinomial data on species detection or nondetection to estimate the probability of occupancy or use of a given sampling unit (MacKenzie et al. 2006). Repeated assessments of each sampling unit additionally allow the

estimation of species detection probability (MacKenzie et al. 2006). We used this statistical approach to estimate the probability of elephant crop depredation from binary conflict data (i.e., HEC reported or unreported). Our sampling sites were 4 km² grid cells. We chose this grid cell size because it was large enough to accommodate an HEC event (i.e., a single HEC event is not attributed to 2 adjacent cells) but not so large as to make inferences on the drivers of elephant crop depredation less meaningful (Guerbois et al. 2012). We used ArcGIS (version 9.3) to overlay a set of 43 such grid cells across the study area, which spanned 172 km² in the agricultural matrix (Fig. 1). We then extracted reported conflicts from within each grid cell during the sampling period and assessed them for detection or nondetection of HEC on a monthly basis. Therefore, one or more reports of HEC from within a grid cell during a month was assigned a 1, while the lack of HEC reports in the cell was assigned a 0. In this manner, we developed detection histories of HEC, in the form of crop depredation, over 77 months (June 2005–October 2011) and across 43 sampled grid cells. During this period, the study area was not sampled for 36 months, and these months were treated as missing values (MacKenzie et al. 2006). Similarly, grid cells that were not surveyed during a given secondary monthly sampling occasion (defined below) were treated as missing data.

We analyzed the HEC data described above with multi-season occupancy models (MacKenzie et al. 2003, 2006). In these models, the occupancy state of sites remains unchanged (or changes randomly) across (k_t) secondary sampling occasions within a primary sampling period

but may change nonrandomly among T primary sampling periods due to colonization or local extinction. We used seasons of crop growth and harvest to define 3 primary periods for each year of our study: fallow season (January–April), when agriculture is limited to household vegetable gardens; jhum crop season (May–August), when sowing, growth, and harvest of crops such as rice, maize, and millet occurs on hill slopes; and paddy crop season (September–December), when wet rice cultivation occurs in flooded valleys (Datta-Roy et al. 2009). Based on the above definition, we partitioned our 77-month detection history into 20 primary periods. Each primary period had 4 secondary monthly sampling occasions (henceforth, secondary occasions), and each month served as a temporal replicate. We expected changes in the occurrence of crop depredation events between primary periods because of the seasonality of crop growth and harvest. Our study included 9 primary periods with no data, during which the grid cells were not sampled. An example detection history is available in Supporting Information.

For the multiseason occupancy modeling, we used program MARK (White & Burnham 1999) implemented in R (R Development Core Team 2013) through the RDOcupEG model in the RMark library (Laake & Rexstad 2007). We estimated the following parameters: probability of detection and reporting of crop depredation in a grid cell during secondary occasion j within primary period t conditional on crop depredation having occurred there ($p_{t,j}$); probability of crop depredation occurrence in a grid cell during the first primary period (ψ_1); probability that a grid cell with no crop depredation in primary period t had crop depredation in primary period $t + 1$ (γ_t); and probability that a grid cell with crop depredation in primary period t did not experience crop depredation in primary period $t + 1$ (ε_t). The parameters γ_t and ε_t are akin to colonization and extinction probabilities in traditional dynamic occupancy studies (MacKenzie et al. 2003).

Our interpretation of ψ within this framework relates to the concept of *use*, defined as the occurrence of a target species—in this case, the occurrence of HEC—within a sampling unit at random points in time (MacKenzie et al. 2006). More specifically, we view HEC as a latent variable, that is the potential for HEC is either present in a location during a season or not. Our ψ parameter refers to the probability that this latent variable assumes the value 1 (HEC potential is present). If that potential is present, then it may be manifested (a realized HEC event may occur), and the resulting event may or may not be detected by our informants. The detection probability we estimated was thus conditional on the latent HEC variable being 1 and is the product of the probability that an HEC event occurred and the probability of detection of such an event given its occurrence.

We began the occupancy modeling by first identifying the most appropriate model structure for $p_{t,j}$ based

on Akaike's information criterion corrected for small sample sizes (AIC_c). Sample size was 358, calculated as the number of surveyed grid cells times the number of primary occasions during which they were sampled. We used distance to major roads (defined as roads accessible by vehicle) and elevation gradient (or ruggedness) as covariates to test the effects of grid cell accessibility on the probability of detection and reporting of crop depredation events. We also allowed $p_{t,j}$ to vary across primary periods. We compared these models to an intercept-only model, where detection probability was constant. During this analysis, we allowed ε_t and γ_t to vary as a function of agricultural season (fallow, jhum, or paddy), primary period, and distance to forest (i.e., distance of grid cell s to the closest forest). Our intention was to use general models for ε_t and γ_t while identifying the best model structure for $p_{t,j}$. We modeled crop depredation in the first primary period (ψ_1) as a constant parameter.

Next, we fixed $p_{t,j}$ to the best supported model structures from the previous analyses and investigated the spatiotemporal drivers of ε_t and γ_t . We used the independent and additive effects of distance to forest; village density; agricultural season; mean rainfall during each primary period calculated with a 2-month time lag ($\bar{R}_{t[-2]}$); and coefficient of variation (CV) of rainfall during each primary period lagged by 2 months ($R_{t[-2]}^{CV}$). We obtained lagged rainfall values by using rainfall estimates 2 months prior to each month of a 4-month primary period to compute rainfall means and CVs for that primary period. We also included pairwise interactive effects of crop season and ruggedness because agriculture in our study area is largely practiced on hill slopes in the jhum season but in valleys in the paddy season. We considered 2-month lags because we expected crop productivity and availability at a given point to be affected by prior rainfall patterns (i.e., during the crop growing period) and because Sukumar (2003) reports a 2-month lag between crop growth and peak crop depredation by elephants.

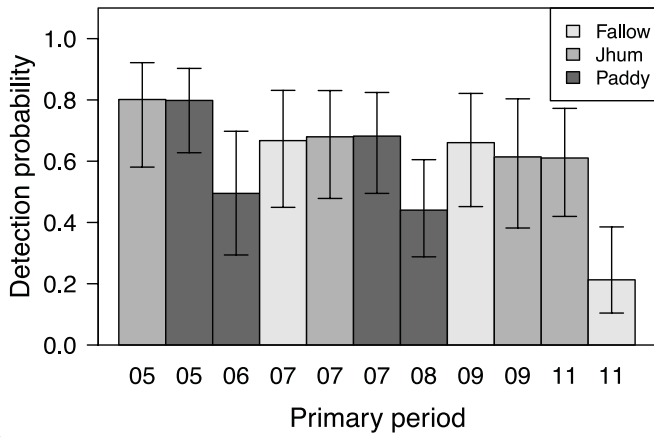
Model comparisons were made on the basis of their AIC_c scores and Akaike weights (w_i). We used the best supported covariates for ε_t and γ_t to estimate predicted probabilities of extinction and colonization of HEC in each of the 3 crop seasons. Based on these estimates, we derived predicted season-specific probabilities of HEC occurrence (ψ_t), which we mapped across the broader landscape to identify areas with a high potential for conflict.

Details on how we obtained our covariate data are provided in the Supporting Information.

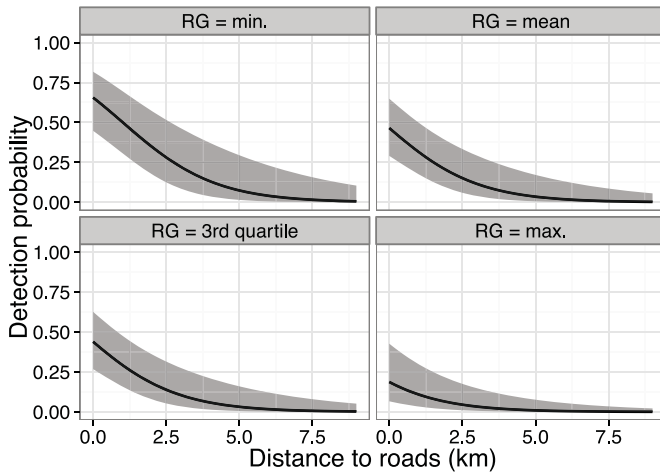
Results

Seasonality of Conflicts

From 2005 to 2011, 636 crop depredation events were reported from agricultural lands belonging to residents of



(a)



(b)

Figure 2. (a) Probability of detection and reporting of crop depredation by elephants adjacent to major roads and at minimum ruggedness within a grid cell during each 4-month primary period (distinct agricultural seasons within each year). Crop seasons (fallow, jhum [shifting cultivation], and paddy) coinciding with the different primary periods are also indicated. (b) Detection probability as a declining function of distance to major roads at minimum, mean, third quartile, and maximum ruggedness (RG). Error bars and shading represent 95% confidence intervals.

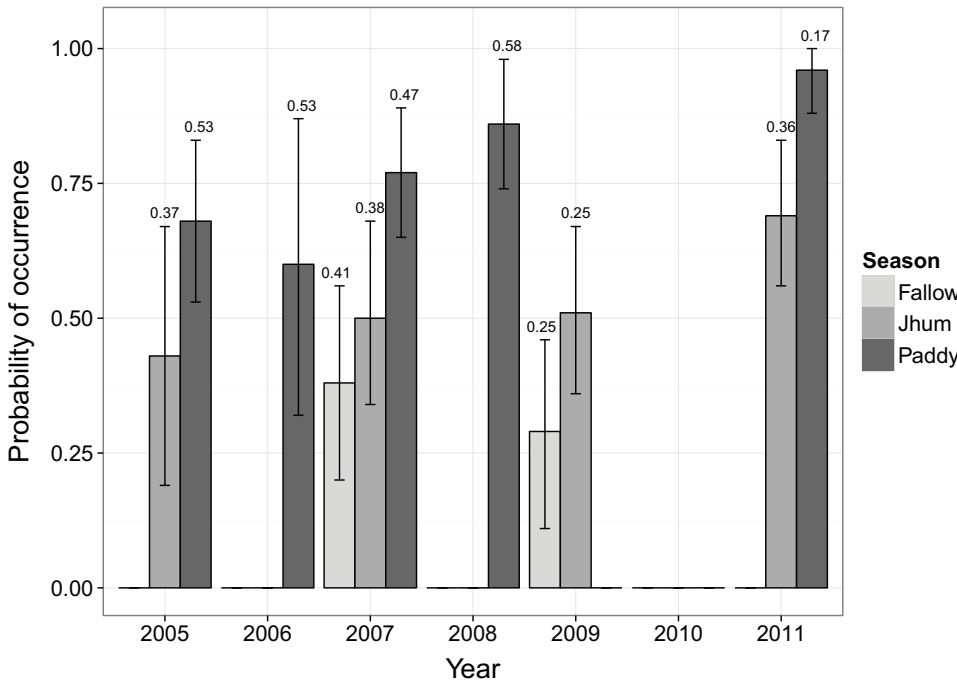


Figure 3. Probability of occurrence of crop depredation by elephants during each sampled 4-month primary period (distinct agricultural seasons within each year) from 2005 to 2011. Crop seasons coinciding with each primary period within a year are indicated. Missing bars coincide with primary periods when there was no sampling. Error bars are 95% confidence intervals, and numbers above each bar represent naïve probabilities of conflict occurrence for each primary period.

the 49 surveyed villages. Annual mean number of conflict reports for the fallow, jhum, and paddy seasons were 38, 76, and 52, respectively. Naïve probabilities of conflict occurrence across primary periods ranged from 0.17 to 0.58 (Fig. 3).

Probability of Reporting Conflicts

The overall probability of detection and subsequent reporting of crop depredation per secondary sampling occasion ($p_{t,j}$) based on the best supported model where this probability was constant was 0.37 (SE 0.03). For this constant $p_{t,j}$ model, the estimate of detection probability per primary occasion combined across the 4 secondary sampling occasions (P^*) was $1 - (1 - p_{t,j})^4 = 0.84$. However, ΔAIC_c between the constant model and the top model for $p_{t,j}$ was 17.61. Models that received maximum support included an additive effect of distance to major roads and ruggedness within a grid cell (Supporting Information). As per the top model, estimates of $p_{t,j}$ from each sampled primary period for grid cells that were adjacent to major roads and had minimal ruggedness ranged from 0.21 (SE 0.07) to 0.80 (SE 0.08) (Fig. 2a). However, $p_{t,j}$ was negatively influenced by both distance to major roads and ruggedness (Table 1, Fig. 2b). We fixed to the 2 model structures (i.e., $p_{t,j} \sim$ major roads + ruggedness, or $p_{t,j} \sim$ major roads + ruggedness + primary period) that had comparable support ($\Delta AIC_c < 2$; Supporting Information) (Burnham & Anderson 2002) while further modeling the crop depredation parameters (i.e., ε_t and γ_t).

Spatiotemporal Patterns of Crop Depredation

Overall estimates of ε_t and γ_t based on the intercept-only model (i.e., a $\varepsilon_t[.]$, $\gamma_t[.]$ model), were 0.29 (SE 0.06) and 0.34 (SE 0.05), respectively. However, there was substantial evidence that spatiotemporal covariates affected both ε_t and γ_t (Supporting Information). Pairwise interactions between crop season and ruggedness played an important role in accounting for the spatiotemporal variation in ε_t ; Akaike weights (w_i) for models that included this effect on ε_t summed to 0.82. In addition, ε_t as per the top model (Supporting Information) was negatively influenced by $\bar{R}_{t[-2]}$ and village density, whereas it was positively influenced by distance to forest (Table 1). The combined negative effects of $R_{t[-2]}^{CV}$ and distance to forest best explained the variation in γ_t (Table 1). However, uncertainty associated with the effect of distance to forest, particularly on γ_t , was substantial. Estimates of ψ_t derived for the sampled primary periods based on the top model (Supporting Information) ranged from 0.29 (SE 0.09) to 0.96 (SE 0.04) (Fig. 3).

The effects of the different spatiotemporal covariates on ε_t and γ_t , and the resultant temporal variation in ψ_t , suggested the following overall trends in elephant crop depredation patterns. Probabilities of crop depredation

occurrence (ψ_t) increased as the crop season transitioned from fallow through jhum to paddy (Fig. 3). For any given transition of season (i.e., fallow to jhum, jhum to paddy, or paddy to fallow) extinction probabilities across years declined with mean rainfall lagged by 2 months ($\bar{R}_{t[-2]}$) (Fig. 4). Extinction probabilities declined marginally as village density increased and demonstrated season-specific variation with ruggedness (Fig. 4). The transition of season from fallow to jhum was associated with high extinction probabilities ($\varepsilon_t \sim 1$) in grid cells with low ruggedness irrespective of $\bar{R}_{t[-2]}$ or village density. In contrast, ε_t was nearly 0 in cells with high ruggedness, although there was greater variation around these estimates when $\bar{R}_{t[-2]}$ was low. As the season transitioned from jhum to paddy, ε_t remained high (>0.9) in rugged cells at $\bar{R}_{t[-2]} \leq 1600$ mm, but decreased steadily thereafter. During this period, ε_t in cells with low ruggedness was negligible (<0.02) when $\bar{R}_{t[-2]} > 2000$ mm. Extinction probabilities did not vary with ruggedness when the season transitioned from paddy to fallow, but it declined when $\bar{R}_{t[-2]}$ and village density decreased. Colonization probabilities declined as variability in rainfall lagged by 2 months increased ($R_{t[-2]}^{CV}$) (Supporting Information). As distance to forests increased, extinction probabilities increased and colonization probabilities decreased, but these effects were characterized by low precision (Table 1).

We used the top model in Supporting Information to predict and map potential ψ for the 3 crop seasons on the basis of site-specific spatial covariates and season-specific estimates of $\bar{R}_{t[-2]}$ and $R_{t[-2]}^{CV}$ averaged across the sampling period between 2005 and 2011. Predicted estimates of ψ increased as the season transitioned from fallow through jhum to paddy and was high in grid cells between PAs (Fig. 5).

Discussion

Occupancy Modeling of Elephant Crop Depredation

The idea of citizen science has emerged from the recognition that certain types of information can only be gathered through a participatory research framework (Kéry et al. 2010). Notwithstanding the value of such a framework, concerns exist about biases arising due to imperfect detection or reporting of the resultant data (Kéry et al. 2010; van Strien et al. 2013). The quantification of HWC largely relies on citizen science data, and failure to account for imperfect detection or reporting of conflicts can lead to flawed inference on the patterns and correlates of HWC. In our study, imperfect detection of a crop depredation event in a spatiotemporal unit arose because villagers failed to detect this event or the event was detected but went unreported. We show how an occupancy-modeling framework can readily

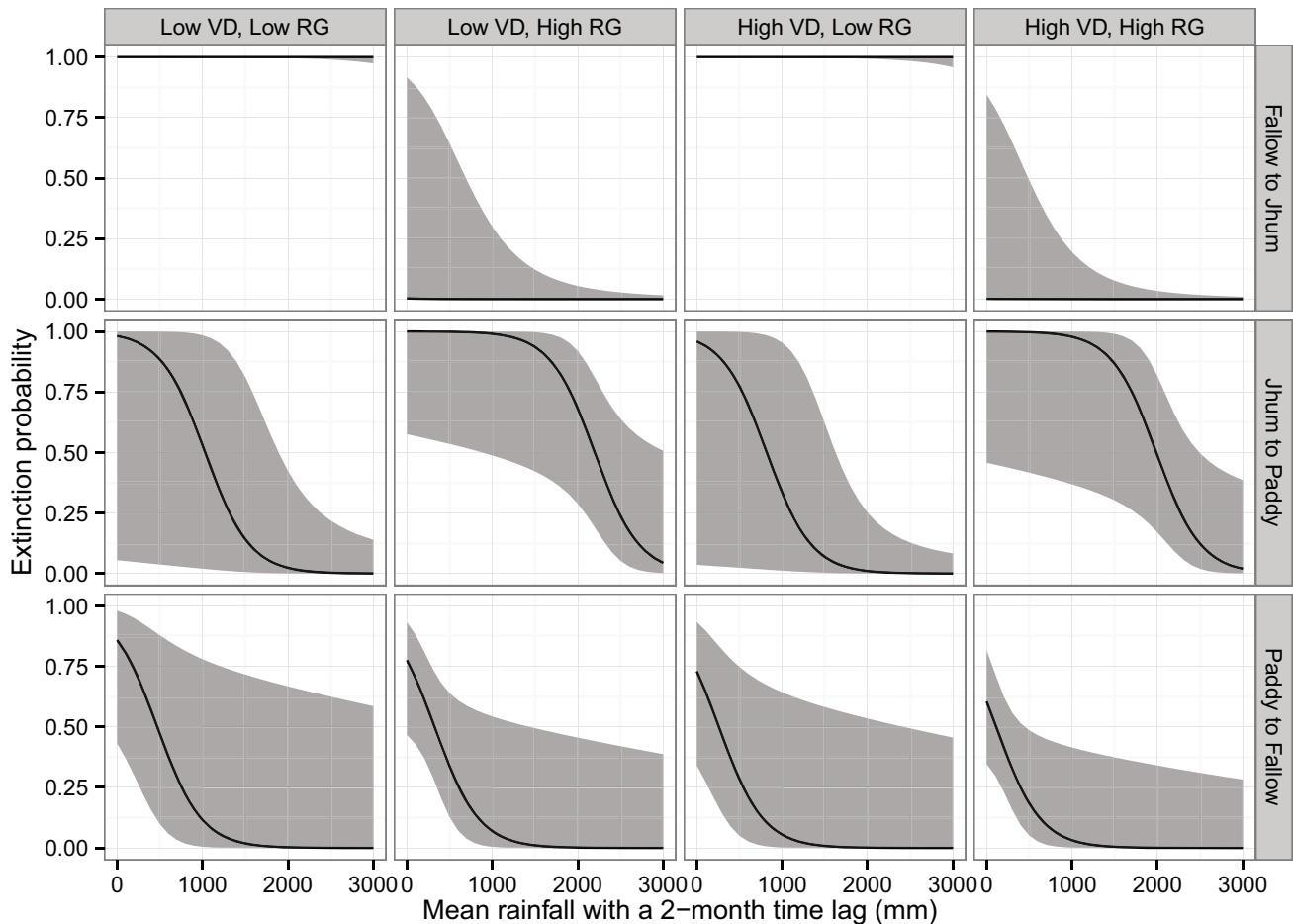


Figure 4. Extinction probability of crop depredation by elephants (i.e., probability that crop depredation occurred in time t but not in time $t + 1$) as a function of mean rainfall, calculated with a 2-month lag, during transitions of season (right axis) for grid cells with low and high village density (VD) and ruggedness (RG). Jhum refers to shifting cultivation. For both ruggedness and village density, low and high levels correspond to their respective first and third quartile values: 12.99 and 16.91 ruggedness index, respectively, and 0.13 and 0.44 villages/km² (village density), respectively. For all plots, distance to forest refuges is set to a mean value of 0.6 km.

incorporate the detection process into existing conflict-reporting systems to account for potential biases at no significant increase in field effort or costs.

The application of the occupancy models to our specific example system broadly suggests that the accessibility of crop fields, and the availability of crops in these fields, is a major driver of elephant crop depredation patterns and dynamics. First, we found strong season-specific signatures in elephant crop depredation patterns. Within a year, crop availability clearly varies among seasons, and this variation was mirrored by an increase in probabilities of crop depredation occurrence (ψ) from the fallow season to seasons of crop growth and harvest (i.e., jhum and paddy seasons) (Fig. 3). Season- and location-specific signatures in HEC extinction probabilities (i.e., probabilities of sites transitioning from experiencing HEC to not experiencing these problems) best explained this seasonal variation in depredation patterns (Supporting Information). The spatial locations of

crops vary by season in our study area, and this variation was evident in season-specific changes in extinction probabilities of elephant crop depredation, particularly when the season transitioned from fallow to jhum. Extinction probabilities were negligible in grid cells with high ruggedness but were very high (~ 1) in cells with low ruggedness (Fig. 4). In contrast, the transition of season from jhum to paddy was associated with high “extinction” probabilities in rugged cells and low “extinction” probabilities in less rugged cells, particularly when rainfall levels were high (Fig. 4). Easier accessibility of crops in the paddy season compared with those grown on hill slopes in the jhum season likely explains the higher occurrence of crop depredation in the paddy season (Fig. 3). This result could also point to a potential preference for paddy as a food resource. Peaks in elephant crop depredation during growing periods of preferred crops have been reported (e.g., Sukumar 2003; Osborn 2004; Gubbi 2012).

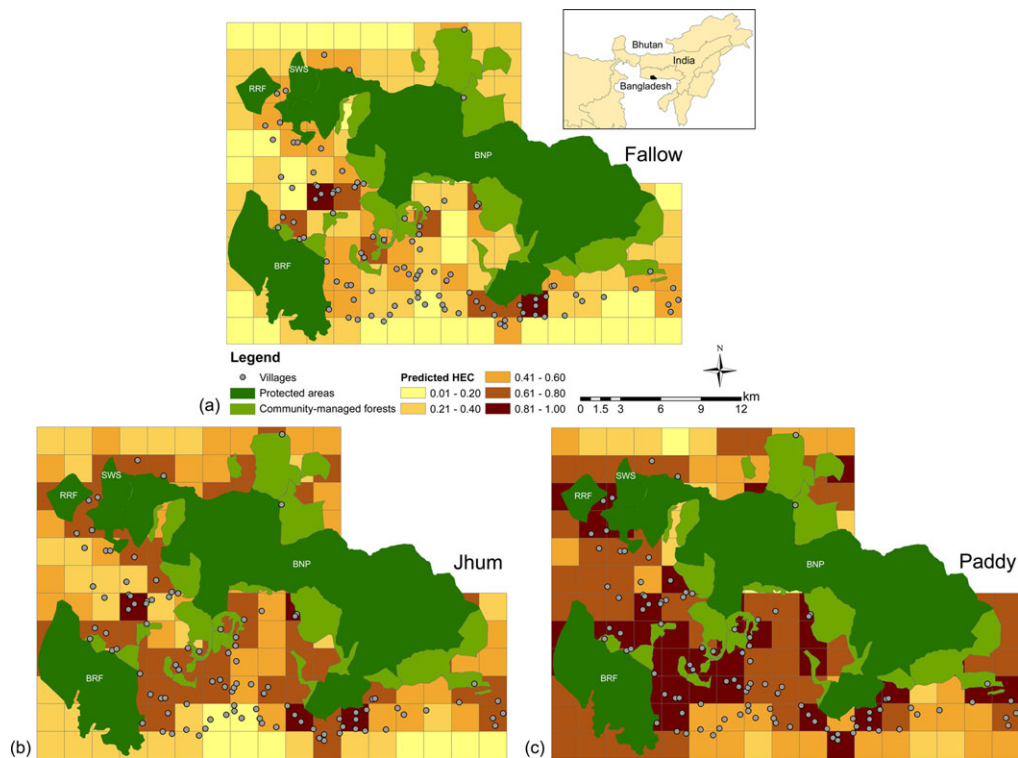


Figure 5. Predicted probabilities of human–elephant conflict (HEC) occurrence across the broader Balphakram–Baghmara landscape in the (a) fallow, (b) jhum (shifting cultivation), and (c) paddy seasons.

Second, for a given transition of season, the probability of elephants not raiding locations that experienced crop depredation previously, declined with an increase in mean rainfall lagged by 2 months (Fig. 4). Furthermore, colonization probabilities of crop depredation (i.e., probabilities of sites transitioning from not being raided by elephants to having crop depredation) decreased as the variability in rainfall lagged by 2 months increased (Supporting Information). Rainfall influences plant phenology and periods of peak forage availability (van Shaik et al. 1993), and irregular rainfall can limit plant resource abundance and introduce unpredictability in forage availability (e.g., Knapp et al. 2002). Therefore, rainfall is conceivably an important driver of crop productivity and availability. Our results are consistent with findings from other sites in Africa and Asia that suggest rainfall-related peaks in elephant crop depredation patterns (Sukumar 2003; Osborn 2004; Webber et al. 2011; Gubbi 2012). The novelty of our study lies in the insights occupancy modeling provided into how rainfall influences the dynamics that underlie these patterns in elephant crop depredation while appropriately accounting for variation in the probability of detecting and reporting crop depredation.

Third, the estimated effects of distance to forest refuges, albeit less precise, were positive on extinction probabilities of elephant crop depredation and negative on HEC colonization probabilities. Furthermore, HEC extinction probabilities declined as village density

decreased. Proximity of crop fields to the forest edge clearly provides greater crop depredation opportunity to elephants. The presence and density of crop fields adjacent to forests can also be expected to increase as village density increases in landscapes such as ours, where local livelihoods are largely agriculture dependent. However, all our sampled grid cells were within 2.5 km of a forest, which is a short distance to traverse for mobile species such as elephants. Observations from both Africa and Asia suggest that elephant crop depredation, although negatively affected by distance to forests, can occur up to 4–6 km from forests occupied by elephants (Gubbi 2012; Guerbois et al. 2012). The relative proximity of our sampled grid cells to the forest edge likely explains the uncertainty associated with the influence of distance to forest refuges on elephant crop depredation dynamics. Moreover, there is an element of risk associated with crop raiding due to human retaliation, and the perception of such risk by elephants is hypothesized to increase with distance from refuges (Graham et al. 2009). Therefore, the observed positive relationship of conflict with village density may not hold for villages far from forests.

Spatial processes beyond those induced by predictors and conflict history of a given sampling unit, may also be important drivers of HWC patterns. There could be neighborhood effects, whereby HWC dynamics in a focal unit are influenced by the incidence of conflict in neighboring units. For example, the mobility of elephants might lead

to the prediction that a spatial unit whose neighbors experienced HEC in season t might be expected to exhibit a higher probability of HEC in season $t + 1$ than a spatial unit whose neighbors were free of conflict at t . We did not consider neighborhood effects on HWC dynamics that go beyond those imposed by chosen spatial covariates. It is, however, possible to explicitly account for the dependence of colonization and extinction rates on neighborhood occupancy within a dynamic occupancy-modeling framework (Yackulic et al. 2012; Eaton et al. 2014). The application of these recently developed autologistic models to conflict data can provide additional insights on the spatial processes and mechanisms that underlie the dynamics of HWC.

Management of HWC

HWC can vary over time and space as a function of factors such as agricultural intensity (Madhusudan 2003) and changes in human and wildlife population densities (Treves & Karanth 2003). The occupancy-modeling framework allowed us to directly model the dynamics of elephant crop depredation as a function of various spatiotemporal covariates. In so doing, we were able to make novel inferences on the mechanisms that underlie changes in conflict patterns over time and across space, rather than limiting our scope of inference to spatiotemporal variation in the patterns themselves. This can inform the design of nuanced and potentially more effective conflict mitigation strategies. For example, extinction probabilities of conflict relate to the persistence of HWC in a particular site; therefore, where or when extinction probabilities are low, reactive management of conflicts may be necessary. In contrast, proactive conflict mitigation measures may be necessary to minimize the colonization of conflict in new areas or over time. The occupancy-modeling framework allowed us to generate such season-specific predictions of conflict occurrence across space (Fig. 5). Moreover, when occupancy studies such as ours are integrated with HWC management, predicted effects of mitigation efforts on extinction–colonization can be tested.

Our specific findings suggest that strategies designed to minimize elephant forays into cultivated lands may be important for HEC mitigation. In the short term, crop-raiding deterrents (e.g., chili pepper fences and spotlights) and physical barriers (e.g., electric fences) may be effective (e.g., Davies et al. 2011). Where possible, land-use zoning in a manner that ensures the cultivation of depredation-prone crops (e.g., paddy and millets) away from forested refugia may be a useful, longer term solution. Predictive maps of conflict occurrence, such as the one we have derived for our study landscape (Fig. 5), can be used to prioritize management by identifying high-risk areas or can inform land-use zoning or spatial conservation planning (Moilanen et al. 2009). Nevertheless,

villages near forests will likely remain susceptible to elephant crop depredation and other forms of HWC. It is imperative therefore to simultaneously undertake measures that can potentially increase tolerance for conflict-prone species and alleviate conflict-induced property and economic loss. These measures could include, for instance, encouraging affected people to report conflicts and improving the processing of compensation claims (Karanth et al. 2013) and offering communal insurance schemes to offset economic losses due to depredation (e.g., Mishra et al. 2003).

The prediction of future conflicts between wildlife and people, and the design of holistic, lasting strategies that can effectively manage these conflicts, hinges on a clear understanding of conflict drivers over time and across space. To that end, we demonstrate the importance of accounting for potential biases arising from imperfect detection or reporting of conflicts. The replicate-specific probability of detection and reporting of elephant crop depredation events in our study was <1.0 , which suggests that an assumption of perfect detectability may not always be valid in HWC research. Explicit modeling of the detection and reporting process is therefore critical to tease apart the spatiotemporal correlates of HWC from factors that drive the process by which these conflicts are observed. For example, we found that detection probability of conflicts was particularly low for sites that were remote and difficult to access (Fig. 2). If we had not accounted for the imperfect detection of conflicts, we may have concluded, for instance, that crop depredation is lower in such sites—a potentially incorrect inference. We therefore strongly recommend the adoption of sampling designs and analytical frameworks that can account for imperfect detection and reporting of conflicts. We are the first to apply an occupancy-modeling framework to the study of HWC. We demonstrate that this approach effectively addresses the issue of imperfect detection, forms a reliable and robust monitoring protocol, and allows for inference on mechanisms underlying spatiotemporal patterns of HWC.

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Supporting Information

An example detection history (Appendix S1), details on how we obtained our covariate data (Appendix S2), model selection tables (Appendix S3), and spatiotemporal variation in conflict colonization probabilities are available online. The authors are solely responsible for the content and functionality of these materials. Queries (other than absence of the material) should be directed to the corresponding author.

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