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RESEARCH ARTICLE*

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Are ranger patrols effective in reducing poaching-related threats within protected areas?

Jennifer F. Moore[1] | Felix Mulindahabi[2] | Michel K. Masozera[2] | James D. Nichols[3] | James E. Hines[3] | Ezechiel Turikunkiko[4] | Madan K. Oli[1]

[1]Department of Wildlife Ecology and Conservation, University of Florida, Gainesville, FL, USA

[2]Rwanda Program, Wildlife Conservation Society, Kigali, Rwanda

[3]United States Geological Survey, Patuxent Wildlife Research Center, Laurel, MD, USA

[4]Rwanda Development Board, Nyungwe National Park, Kitabi, Rwanda

Correspondence
Jennifer F. Moore
Email: jennmoore924@ufl.edu

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Department of Wildlife Ecology and Conservation, University of Florida, Wildlife Conservation Society Rwanda Program, and the Rwanda Development Board.

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Abstract

1. Poaching is one of the greatest threats to wildlife conservation world-wide. However, the spatial and temporal patterns of poaching activities within protected areas, and the effectiveness of ranger patrols and ranger posts in mitigating these threats, are relatively unknown.
2. We used 10 years (2006–2015) of ranger-based monitoring data and dynamic multi-season occupancy models to quantify poaching-related threats, to examine factors influencing the spatio-temporal dynamics of these threats and to test the efficiency of management actions to combat poaching in Nyungwe National Park (NNP), Rwanda.
3. The probability of occurrence of poaching-related threats was highest at lower elevations (1,801–2,200 m), especially in areas that were close to roads and tourist trails; conversely, occurrence probability was lowest at high elevation sites (2,601–3,000 m), and near the park boundary and ranger posts. The number of ranger patrols substantially increased the probability that poaching-related threats disappear at a site if threats were originally present (i.e. probability of extinction of threats). Without ranger visits, the annual probability of extinction of poaching-related threats was an estimated 7%; this probability would increase to 20% and 57% with 20 and 50 ranger visits per year, respectively.
4. Our results suggest that poaching-related threats can be effectively reduced in NNP by adding ranger posts in areas where they do not currently exist, and by increasing the number of patrols to sites where the probability of poaching activities is high.
5. *Synthesis and applications*. Our application of dynamic occupancy models to predict the probability of presence of poaching-related threats is novel, and explicitly considers imperfect detection of illegal activities. Based on the modelled relationships, we identify areas that are most vulnerable to poaching, and offer insights regarding how ranger patrols can be optimally deployed to reduce poaching-related threats and other illegal activites, while taking into account potential sampling biases. We show that poaching can be effectively reduced by increasing ranger patrols to areas under high risk of poaching activities, and by adding ranger patrols near these sites. These findings are broadly applicable to national parks and protected areas experiencing a high degree of poaching and other illegal activities.

KEYWORDS
Albertine Rift, dynamic occupancy models, Nyungwe National Park, poaching, ranger-based monitoring, Rwanda, snares, spatial threat patterns, temporal threat patterns

1 | INTRODUCTION

Illegal human activities (e.g. poaching and natural resource extraction) often represent the single most important challenge to wildlife conservation and protected area management (Effiom, Nunez-Iturri, Smith, Ottosson, & Olsson, 2013; Martin & Caro, 2012). These anthropogenic threats are often correlated with human population growth and poverty levels, with protected areas situated in regions characterized by rapidly growing, poverty-stricken human populations generally facing the highest levels of threats (Butchart et al., 2010; Challender & MacMillan, 2013; Craigie et al., 2010). Effective management of protected areas and law enforcement to mitigate these threats are vitally important for global biodiversity conservation (Brandon, Redford, & Sanderson, 1998; Dudley & Stolton, 2008). However, managing anthropogenic threats to wildlife often depends on cultural, social and economic contexts, and there is no single solution that is likely to be appropriate for all regions (McNeely, Harrison, & Dingwall, 1994).

In many protected areas, poaching is the largest threat to wildlife, and has been shown to be the cause of population declines as well as shifts or reductions in distributional range of many species (Newmark, 2008; Stoner et al., 2007). Poaching can also have cascading effects across trophic levels, can alter structure and functions of ecological communities and ecosystems, and potentially can affect ecosystem services offered by many protected areas (Brodie, Helmy, Brockelman, & Maron, 2009; Estes et al., 2011; Lawlor, 1979; Paine, 1980). Poaching occurs for three primary reasons. First, animals are poached in retribution for livestock predation (e.g. Kissui, 2008; Oli, Taylor, & Rogers, 1994) or crop raiding (Desai & Riddle, 2015; Goswami, Medhi, Nichols, & Oli, 2015). Second, hunters will poach wildlife species within protected areas for bushmeat, as a source of protein in poor communities that do not have access to alternative and affordable protein sources. Finally, poachers kill wildlife to supply demands for illegal wildlife products and trade, mostly to wealthy countries (Lindsey et al., 2013). The illegal wildlife trade alone (excluding small-scale subsistence bushmeat hunting) is estimated to be worth US$20 billion globally (Challender & McMillan, 2013); thus, fully eradicating poaching would be challenging, if not impossible, requiring cooperation among governments and conservation organizations across the globe. However, effective anti-poaching management programmes in each protected area would be a necessary first step in combating poaching-related threats to global biodiversity conservation.

Attempts have been made to quantify poaching through surveys of bushmeat sold in markets and villages (Edderai & Dame, 2006; Fa et al., 2006), household or hunter questionnaire surveys (Lindsey et al., 2011; Moro et al., 2012), and arrest records from protected areas (Ijeomah, Ogogo, & Ogbara, 2013; Knapp, Rentsch, Schmitt, Lewis, & Polasky, 2010; Risdianto et al., 2016). These methods can lead to biased inference, as market and village surveys only measure supply, and not necessarily demand or source of bushmeat. Household and hunter questionnaires can underestimate poaching activity due to fear of being reported for illegal activity, and arrest records can be confounded by the effort put forth by law enforcement (Moro et al., 2012; St John et al., 2012). An alternative to these indirect methods would be to directly measure poaching-related threats within national parks or protected areas (Critchlow et al., 2015; Plumptre et al., 2014; Watson, Becker, McRobb, & Kanyembo, 2013). Direct quantification of poaching-related threats has the potential to yield unbiased estimates if a probabilistic (e.g. random or stratified random) sampling protocol is followed and probability of detection is taken into account. It is highly unlikely that researchers or rangers will detect all poaching-related activities that are present within a surveyed area (Critchlow et al., 2015; Keane, Jones, & Milner-Gulland, 2011; Nguyen et al., 2016). Failure to account for imperfect detection can potentially lead to incorrect or biased inference (Goswami et al., 2015; MacKenzie et al., 2006; Williams, Nichols, & Conroy, 2002).

Using 10 years of data on poaching-related threats collected in Nyungwe National Park (NNP), Rwanda by park rangers while on patrol, our objectives were to: (1) quantify spatio-temporal patterns of poaching-related threats in NNP, (2) discern spatial factors that affect detection and dynamics of these threats and (3) develop a threat map showing the probability of poaching-related threats based on spatial characteristics. In particular, as a part of (2), we aimed to directly investigate the relationships between various management actions (e.g. number of ranger patrols and locations of ranger posts) and threat dynamics; such relationships permit predictions needed to inform management decisions. Data collected by rangers while on patrol have previously been used to assess illegal activities within protected areas in Uganda, Democratic Republic of Congo, Rwanda, Sumatra and India among others (Critchlow et al., 2015; Gray & Kalpers, 2005; Linkie et al., 2015; Mackenzie, Chapman, & Sengupta, 2011; Stokes, 2010). However, whether and to what extent ranger patrols reduce poaching-related threats generally remains untested. Thus, we also sought to (4) evaluate the efficacy of ranger patrols in reducing poaching-related threats in NNP. We used dynamic occupancy models to analyse the data (MacKenzie et al., 2002, 2003) because they provide a rigorous statistical framework for estimating relevant parameters while also accounting for imperfect detection of threats by rangers (Goswami et al., 2015; Linkie et al., 2015; MacKenzie et al., 2006; Sharma, Wright, Joseph, & Desai, 2014).

We hypothesized that: (1) the probability of occurrence of poaching-related threats will be the highest in easily accessible areas of NNP, such as along the park boundary, near roads and tourist trails, and in areas of low elevation. These areas tend to be close to human habitation, and thus are the closest and easiest places to access the park for poaching and other illegal activities (Plumptre et al., 2014; Watson et al., 2013); (2) poaching threats would be lower in areas closer to the ranger posts because presence of rangers in these posts generally deters illegal activities; and for the same reason, (3) probability of extinction of poaching-related threats in an area would be positively influenced by the number of ranger patrols.

2 | MATERIALS AND METHODS

2.1 | Study area

This study was conducted in NNP, a tropical, montane forest located in southwestern Rwanda (Figure 1). Together with Kibira National Park, Burundi, the Nyungwe-Kibira landscape is the largest remaining montane forest in Africa (Plumptre et al., 2002). The main forest block of Nyungwe is 970 km^2 in size, ranges in elevation from 1,451 to 2,950 m and covers a range of habitat types including rainforest, bamboo forest, savanna and swamp (Plumptre et al., 2002). Nyungwe is a biodiversity hotspot because it harbours several endemic and globally threatened species such as the endangered eastern chimpanzee (*Pan troglodytes schweinfurthii*; Plumptre et al., 2007). It is presumed to be home to 85 mammals, 275 birds, 32 amphibians, 38 reptiles and 1,058 plant species (Plumptre et al., 2002).

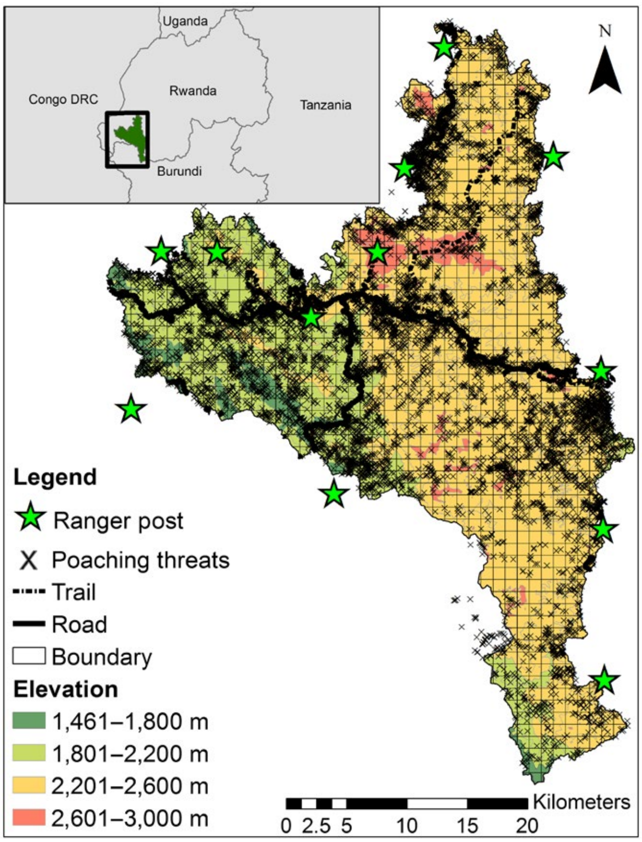

FIGURE 1 Nyungwe National Park, Rwanda showing the 1-km^2 grid cells (which served as study sites), the elevation categories, roads, trails, ranger posts, park boundary and the locations of detected poaching-related threats [Colour figure can be viewed at wileyonlinelibrary.com]

2.2 | Field methodology

Ranger-based monitoring (RBM) programmes are implemented in many protected areas because they are more cost-effective and financially feasible than long-term and independent monitoring and law enforcement programmes (Gray & Kalpers, 2005; Keane et al., 2011). A RBM programme was initiated in NNP in 2006, and continues to date. Rangers had a minimum of 3 years of experience before the initiation of this programme; rangers hired since 2006 were trained by the original rangers. The objectives of ranger patrols were to (1) detain poachers (or those involved in other illegal activities) within the park, (2) destroy or remove snares or other means of poaching and (3) collect data on all illegal activities. They recorded the type and magnitude of illegal activities they encountered, including evidence of poaching, forest product extraction, livestock, agriculture, honey extraction, fire and mining. For this study, we used data collected on poaching-related illegal activities, which included wire, metal, and rope snares, poachers' camps, and arrest and detention of poachers.

Park rangers were sent on patrol in NNP during the day and at night, with an average of 6–7 patrols per day. Each patrol consisted of 4–6 rangers hired by the government; patrols in later years were also accompanied by a community informant (or an ex-poacher), about once a month. The target location for each patrol was determined by the head ranger for each management sector of the park, and rangers could follow any route to and from that location. Data collected by rangers were stored and managed using the Management Information System (MIST) database (Stokes, 2010).

We applied a dynamic multi-season occupancy modelling framework (MacKenzie et al., 2003, 2006) to these data to estimate the probability of occupancy (probability that poaching-related threats are present in a site), colonization (probability that poaching-related threat are present in an area in year $i + 1$, given that they were not present in year i) and extinction (probability that poaching-related threats were not present in year $i + 1$, given that they were present in year i) of poaching threats within NNP. This framework requires a set of sites, at least some of which are visited multiple times, as well as detection/non-detection data on threats associated with those visits. We divided NNP into 1,169 grid cells of up to 1 km^2 in size (hereafter, "sites"); some sites along the park boundary were <1 km^2 in size due to the irregular shape of the park (Figure 1). Each time a ranger patrol visited a site, it was given a value of 1 if at least one poaching-related threat was detected, or 0 if no poaching-related threat was detected. Each year of study (2006–2015) was considered a primary period (i) and each ranger patrol within a year was considered a secondary occasion (j). The number of secondary occasions varied each year, corresponding to the maximum number of times a ranger patrol entered any one site during that year; sites receiving fewer than the maximum number of visits for a given year were assigned missing values. Thus, our detection histories consisted of 1s or 0s (detection/non-detection), or missing data (–) for sites that were visited fewer than the maximum number of times that year.

Multi-season occupancy models usually assume "closure" across the secondary periods (i.e. ranger visits) that comprise each primary period (i.e. year; MacKenzie et al., 2003, 2006). In this study, we viewed occupancy of a site as "use," in the sense that we did not assume that poaching was occurring throughout the entire primary period (year) at an occupied site. Instead, we viewed an occupied site as threatened by poaching throughout the year, with actual poaching activity occurring at random times within each year. A related issue is the absence of a clear time interval with no sampling to which the extinction and colonization parameters pertain. We explored the data trying to identify periods of the year that contained a large fraction of sampling occasions, with the idea that we would define a portion of each year as the annual primary sampling period. However, ranger patrols were distributed throughout the year, so identifying a specific period of the year would have resulted in substantial loss of data. We thus followed the approach sometimes used in band recovery (Smith & Anderson, 1987) and open capture–recapture modelling of treating the entire year as a primary sampling period and viewing local extinction and colonization parameters as corresponding to the period from the mid-point of 1 year (e.g. 1 July) to the mid-point of the next. This approach is not ideal, but was necessitated by our use of ranger patrol survey data rather than data from a designed sampling programme.

If rangers detected illegal activities or sighted wildlife while on patrol, they obtained GPS locations at those sites. When illegal activities were not detected or wildlife were not observed, rangers recorded GPS locations every 30 min. Based on these GPS locations, we created the most likely trajectory followed by each ranger patrol. These trajectories were used to determine the number of patrols received by a site for each year of the study.

For each site, we calculated the following covariates: (1) minimum and maximum elevation category (1,461–1,800, 1,801–2,200, 2,201–2,600 and 2,601–3,000 m; continuous elevation data were not available); (2) distance to the nearest ranger post (M = 5,203 [SE 77]; range: 0–12,025 m), nearest road (M = 6,107 [SE 219]; range: 0–31,067 m), nearest tourist trail (M = 6,953 [SE 218]; range: 0–32,221 m) and nearest park boundary (M = 1,991 [SE 69]; range: 0–9,595 m); and (3) the number of ranger visits (0–87 visits per year; Figure 1). All distances were calculated using ArcGIS version 10.4 (ESRI, 2011). Distance to anthropogenic features and elevation categories were used as site-specific covariates. Each ranger visit to a site was viewed as a sampling occasion (i,j denoting occasion j of year i) and was used to draw inferences about detection. For the modelling of threat occupancy, extinction and colonization, the number of ranger visits was a time-varying, site-specific covariate, and was calculated by mapping the daily patrols in ArcGIS (ESRI, 2011), and summing the number of times a patrol visited each site. The continuous covariates were all standardized to a mean of zero and standard deviation of one by subtracting the mean and dividing by the standard deviation. We did not consider additive or interactive effects of multiple covariates on model parameters due to multicollinearity between covariates and insufficient data to support more complex model structures.

We used the initial parameterization of the multi-season occupancy model (MacKenzie et al., 2006), which allowed us to estimate the following parameters: (1) ψ_{2006}, initial occupancy, or the probability that a poaching-related threat existed in a site at the beginning of the study period (year 2006); (2) ϵ_i, extinction probability, or the probability that poaching-related threats were not present in year $i + 1$, given that they were present in year i; (3) γ_i, colonization probability, or the probability that poaching-related threats were present in year $i + 1$, given that they were not present in year i; and (4) $p_{i,j}$, detection probability for occasion j in year i, probability that poaching-related threats are detected at a site containing threats in year i. More specifically, given that threats occur at a site during year i, $p_{i,j}$ represents the product of (1) the probability that threats are present during sampling occasion j and (2) the probability that at least one threat is detected given presence at occasion j. We modelled the threat-related parameters (ψ_{2006}, ϵ_i and γ_i) as possible functions of minimum elevation category or maximum elevation category, as well as the distance to boundary, road, trail and ranger posts. Additionally, we allowed ϵ_i and γ_i to be affected by the number of ranger visits in year i. We allowed $p_{i,j}$ to be affected by the area of the site, the year (i) of the study, as well as the additive effect of area and year.

We estimated unconditional occupancy probabilities (ψ_i) for each year i (the probability that a threat is present in a site in year i) as a derived parameter using the following recursive equation (MacKenzie et al., 2006):

$$\psi_i = \psi_{i-1}(1-\epsilon_{i-1}) + (1-\psi_{i-1})\gamma_{i-1}.$$

Using the most parsimonious model (Table 1), we estimated the probability of poaching-related threats for each site for 2016. We then mapped these values using ArcGIS (ESRI, 2011) to develop a "risk map," which displays the probability of occurrence of poaching-related threats for each site in 2016.

We used an information-theoretic approach using the Akaike information criterion corrected for small sample size (AIC_c) for statistical inference and to select the most parsimonious model in the candidate model set (Burnham & Anderson, 2002). The influence of a covariate on model parameters was evaluated by comparing models with and without that covariate, and by checking to see if the 95% confidence interval (95% CI) for the regression coefficient (β parameter) included zero. Models were run in program MARK (White & Burnham, 1999) using the *RMark* package version 2.2.0 (Laake, 2013) in the R computing environment version 3.3.1 (R Development Core Team, 2015).

3 | RESULTS

Over our study period (2006–2015), 17,785 ranger patrols were deployed, and 39,463 poaching-related threats were detected (mean number of threats per site per year = 4.24 [SE 0.14]; range: 0–344; Figure 2). The spatial locations of all poaching-related threats detected during the study period are displayed in Figure 1. The maximum number of ranger patrols to a site in a single year was 87 (M = 10.9 [SE 0.04]). The total number of ranger patrols increased over time with more patrols in the later years (Figure 2).

Ignoring the effect of covariates ($\psi_{2006}(.)\epsilon(.)\gamma(.)p(.,.)$), the overall estimated probability that poaching-related threats occurred at any site at the beginning of the study period (initial occupancy; ψ_{2006}) was 0.69 [SE 0.03]. The probability that poaching-related threats were not present in a site in 1 year, given that they were present the previous year (probability of extinction; ϵ) was estimated to be 0.15 (SE 0.01), and the probability that poaching-related threats were present in a site in 1 year,

TABLE 1 Model comparison statistics for multi-season occupancy models testing for covariate effects on initial occupancy (ψ_{2006}), probability of extinction (ϵ_i), probability of colonization (γ_i) and detection probability ($p_{i,j}$). Model structure, number of parameters, AIC_c (Akaike information criterion corrected for small sample size) statistic, ΔAIC_c (difference in AIC_c statistic between top model and a selected model) and model weight are also given. Models with ΔAIC_c <10 are presented. See Appendix S1 for top 100 models

Model[a]	npar	AIC_c	ΔAIC_c	Weight
ψ_{2006}(minE)ϵ(rvst)γ(boundary)*p*(year + area)	19	38,559.53	0.00	0.81
ψ_{2006}(boundary)ϵ(rvst)γ(boundary)*p*(year + area)	17	38,565.29	5.76	0.04
ψ_{2006}(rangepost)ϵ(rvst)γ(boundary)*p*(year + area)	17	38,565.31	5.78	0.05
ψ_{2006}(1)ϵ(rvst)γ(boundary)*p*(year + area)	16	38,565.45	5.92	0.04
ψ_{2006}(road)ϵ(rvst)γ(boundary)*p*(year + area)	17	38,566.42	6.90	0.03
ψ_{2006}(trail)ϵ(rvst)γ(boundary)*p*(year + area)	17	38,566.60	7.08	0.02
ψ_{2006}(maxE)ϵ(rvst)γ(boundary)*p*(year + area)	19	38,568.90	9.38	0.01

[a]Covariates are: minE (minimum elevation category), rvst (number of ranger visits during year *i*), boundary (distance to park boundary [m]), year (year of study), area (size of study site [m^2]), ranger post (distance to nearest ranger post [m]), road (distance to nearest road [m]), trail (distance to nearest trail [m]) and maxE (maximum elevation category).

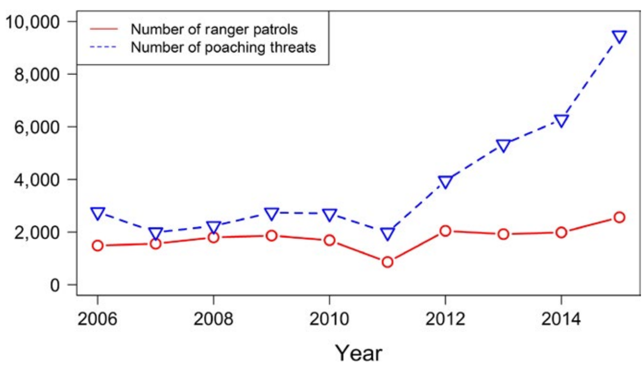

FIGURE 2 The total number of ranger patrols and the total number of poaching-related threats (ignoring imperfect detection) encountered each year of the study (2006–2015) in Nyungwe National Park, Rwanda [Colour figure can be viewed at wileyonlinelibrary.com]

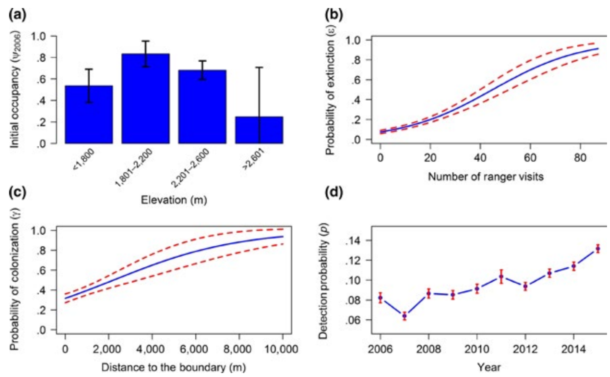

FIGURE 3 Parameter estimates and the influence of covariates based on the top-ranked model from the candidate model set (see Table 1). (a) The probability of occurrence of a poaching-related threat at the beginning of the study period (ψ_{2006}) based on elevation category; (b) the probability of poaching-related threats not being present in a site during year *i* + 1 given threats were present in year *i* (ϵ_i) based on the number of ranger patrols in year *i*; (c) the probability of poaching-related threats being present in a site in season *i* + 1 given threats were not present in season *i* (γ_i) based on the distance of the site to the park boundary; (d) the temporal trend in the probability of detecting a poaching-related threat during a ranger visit given that the threat is present ($p_{i,j}$), for each year of the study for a site of average size [Colour figure can be viewed at wileyonlinelibrary.com]

given they were not present in the previous year (probability of colonization; γ) was estimated at 0.40 (*SE* 0.02). Finally, the probability of detecting poaching-related threats during each ranger patrol when they were present (detection probability; *p*) was estimated to be 0.10 (*SE* 0.002).

In terms of covariates, the most parsimonious model (i.e. the model with the lowest AIC_c value) included the effect of: minimum elevation category on ψ_{2006}; number of ranger visits on ϵ_i; distance to boundary on γ_i; and an additive effect of year and grid cell size on p_i (Table 1; weight = 0.81; top 100 models included in Appendix S1). Based on the most parsimonious model, (1) ψ_{2006} ranged from 0.25 (*SE* 0.23) at the highest elevation zone (2,601–3,000 m) to 0.83 (*SE* 0.06) at the mid-elevation (1,801–2,200 m) zone (Figure 3a); (2) ϵ_i was positively influenced by the number of ranger visits to a site in year *i* (Table 2; Figure 3b); (3) γ_i was positively influenced by the distance to the park boundary (Table 2; Figure 3c); and (4) $p_{i,j}$ varied over time ranging from 0.06 (*SE* 0.005) in 2006 to 0.13 (*SE* 0.004) in 2015 (Figure 3d). The sites that were 1 km^2 in size had a marginally higher detection probability than the sites along the boundary of <1 km^2 in size.

Because covariates chosen for our analyses had management implications, we also considered singular effects of covariates even if they were not included in the most parsimonious model. We used the top model (based on AIC_c scores) containing each covariate for these results. We found that ϵ_i was positively influenced by the distance to roads and trails, but negatively influenced by the distance to the park boundary and ranger post (Table 2). The effect of these covariates on γ_i was the opposite, with γ_i being negatively influenced by the distance to roads and trails, but positively influenced by the distance to the park boundary and ranger post (Table 2). Additionally, ϵ_i was the highest in the lowest elevation zone (1,461–1,800 m), and γ_i was the highest in the mid-elevation zone (1,801–2,200 m). There was no discernible effect of number of ranger patrols on γ_i.

TABLE 2 The effect of covariates on the probability of extinction (ϵ_i) and probability of colonization (γ_i). The regression coefficients (β) with confidence intervals (in parentheses) based on the top-ranked model that included a particular covariate are presented for each parameter. See Table 1 for a description of covariates

Model parameter	Distance to road	Distance to boundary	Distance to trail	Distance to ranger post	Number of ranger visits
ϵ_i	0.39 (0.26, 0.51)	−0.98 (−1.22, −0.73)	0.40 (0.27, −0.53)	−0.39 (−0.55, −0.23)	*0.52 (0.43, 0.62)*
γ_i	−0.32 (−0.44, −0.19)	*0.82 (0.50, 1.13)*	−0.33 (−0.47, −0.19)	0.51 (0.30, −0.72)	−0.001 (−0.01, 0.10)

Values in italics denote the covariates included in the most parsimonious model (Table; weight = 0.81).

The unconditional probabilities of poaching-related threats predicted for 2016 based on parameters estimated from the most parsimonious model (weight = 0.81, Table 1) ranged from 0.10 to 0.97 (Figure 4). The sites with the highest probabilities of poaching-related threats were in the southern portion of the park near Burundi, while the sites with the lowest probabilities of poaching-related threats were near the park boundary, especially around ranger posts.

4 | DISCUSSION

Poaching is a global concern and is thought to be one of the primary causes of population declines of many wildlife species throughout the world (Newmark, 2008; Stoner et al., 2007); yet, spatial and temporal patterns of poaching remain largely unknown. Using RBM data and a dynamic occupancy modelling framework, our goal was to quantify spatial and temporal patterns of poaching-related threats and to discern factors influencing such threats within NNP, Rwanda. The occupancy modelling framework allowed us to directly quantify poaching-related threats, taking into account uneven sampling (both temporally and spatially) as well as imperfect detection while evaluating factors influencing the threats (MacKenzie et al., 2006).

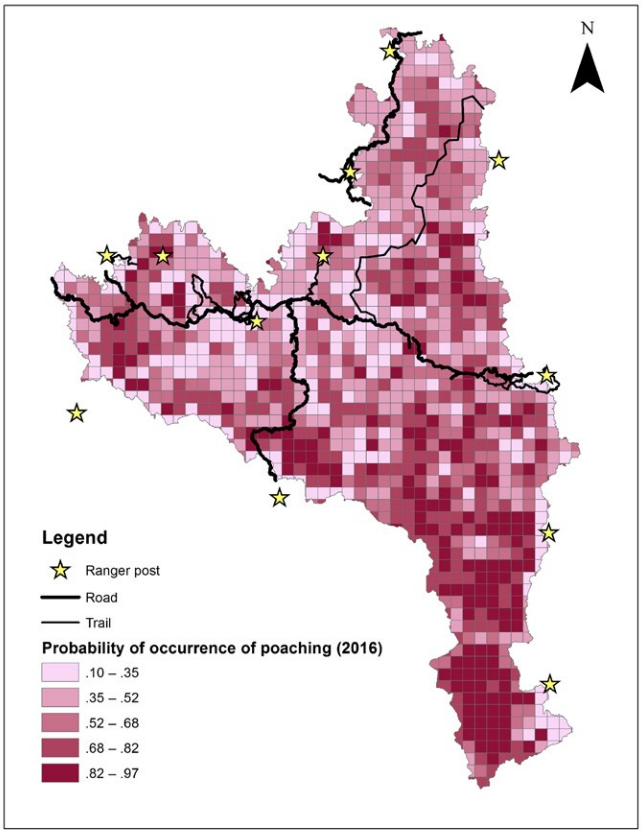

FIGURE 4 The projected probability of occurrence of poaching-related threats for 2016 derived from estimates of initial occupancy, probability of colonization and extinction, and the associated covariates based on the highest ranked model from Table 1 [Colour figure can be viewed at wileyonlinelibrary.com]

During our study, >1,900 poaching-related threats were detected in NNP each year, with the number of threats detected increasing over time to more than 9,000 in 2015 (Figure 2). These threats were distributed throughout the national park, but occurred in high numbers in the west and northwest portion of the park (Figure 1). Fewer threats were detected in the southern and central east portions of the park. This low encounter with threats was because of inaccessibility of these areas and potential violence due to unrest in neighbouring Burundi. However, we cannot rule out the possibility that few poaching-related activities occurred in these areas because little natural vegetation remains in this region due to arson fires, thus potentially eliminating the habitat for some species. Overall, the probability that poaching-related threats occurred in a randomly selected cell within NNP at the beginning of the study period was 69%; this probability decreased to 58% in 2016 (Figure 5). However, the raw count of poaching-related activities and the naïve threat occupancy increased over the study period (2,759 threats or *c.* 20% naïve occupancy in 2006 to 9,473 threats or *c.* 51% naïve occupancy in 2015). Even though the raw count and naïve occupancy of threats were higher in the later years, the overall probability of occurrence of poaching-related threats was lower because detection probability increased over time (Figure 3d). Without accounting for imperfect detection, we would have erroneously concluded that poaching-related threats increased in NNP during our study (Figure 2).

Estimated probability of detection during a ranger patrol ranged from 6% in 2007 to 13% in 2015. When coupled with a low number of secondary sampling occasions, a low detection probability can lead to an overestimated occupancy probability (MacKenzie & Royle, 2005; MacKenzie et al., 2002). Although the probability of detection in our study was <15%, we had a fairly large number of secondary occasions (≥31), which positively affects the overall detection probability for each year. To illustrate, the overall probability of detection (probability that threats are detected on at least one occasion at a site, given that threats occur at the site) for a primary sampling period can be computed as $p_i = 1-(1-p_{i,j})^K$, where K is the number of secondary occasions in a given year. Thus, for $p_{i,j}$ = 0.10 *and* 31 occasions,

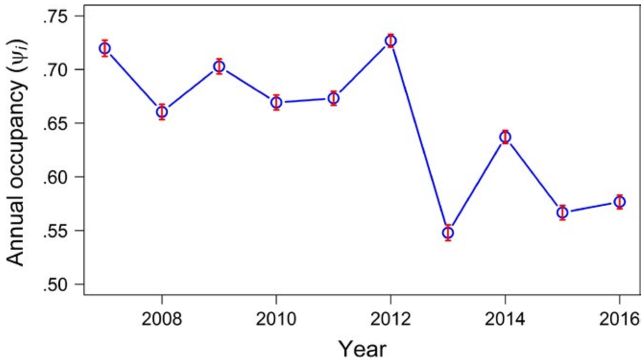

FIGURE 5 The average annual probability of occupancy of poaching-related threats at a randomly selected site in NNP for 2007–2016 derived from the highest ranked model from Table 1. Annual occupancy ($\psi_i = \psi_{i-1} \times (1-\varepsilon_{i-1}) + (1-\psi_{i-1}) \times \gamma_{i-1}$) was estimated as a derived parameter for each site using site-specific covariate values (see Table 1 for parameter definition) [Colour figure can be viewed at wileyonlinelibrary.com]

$p_i \approx 0.96$, so our estimates of dynamic occupancy parameters should be approximately unbiased, even with low detection probability during each ranger visit. The increase in detection probability over the study period suggests that the rangers' ability to find poaching-related activities improved as they gained more experience, or that the density of threats within the site increased over time (or a combination thereof). An increase in the average number of rangers per patrol could also potentially lead to higher detection probability; however, the average number of rangers per patrol did not change during our study.

The probability of poaching-related threats being present in 2006 as well as the probability of colonization of threats was higher near roads and trails. Because these features make the park more accessible, poachers are likely to use these paths to enter the forest (Plumptre et al., 2014; Watson et al., 2013). Thus, we expected a higher occurrence of threats near the park boundary (i.e. closer to human habitations). Contrary to our expectation, based on the probability of colonization and extinction of poaching-related threats, there was a lower probability of threats closer to the park boundary. Although villages are located around the park, the majority of ranger posts are also located near the park boundary; thus, poachers would be more likely to be apprehended if engaged in illegal activities near the edge of the park. This explanation is also consistent with our finding that the probability of occurrence of poaching-related threats is negatively influenced by distance to ranger posts where ranger patrols originate; thus, areas around ranger posts are by default heavily patrolled.

Efficient law enforcement and basic management actions can directly enhance conservation success in the long term (Laurance et al., 2012; Lindsey et al., 2013). Our study shows that increasing ranger patrols reduced the probability of poaching-related threats given that they were present in the previous year (ϵ_i) within the park. Estimated threat extinction probability for sites that are not visited by ranger patrols is 7%; this probability would increase to 12%, 20% and 57% with 10, 20 and 50 ranger visits per year, respectively. Thus, increasing the average number of ranger patrols per site to about 20 per year would almost double the probability of threat extinction (Figure 3d).

Increasing ranger patrol efficiency by prioritizing sites experiencing high threats (Figure 4) has the potential to reduce threats in a manner that is more cost-effective and logistically feasible (also see Hofer, Campbell, East, & Huish, 2000; Plumptre et al., 2014). To identify areas with high poaching-related threats, we developed a threat map using dynamic occupancy parameters estimated from the top model (Figure 4). Our threat map revealed that the southern region of the park and areas along the border with Burundi experience the highest probability of poaching-related threats. Based on these results, and our findings that the occurrence of poaching-related threats is lower in close proximity to ranger posts and with increased ranger visits, we suggest adding ≥1 post in the southern portion of the park and increasing ranger visits to this region. A previous study from the Serengeti showed that mapping the probability of occurrence of poaching activity was an effective way to identify target locations for law enforcement patrols (Hofer et al., 2000), and a study from the Greater Virunga Landscape used threat detections to select sites for prioritizing law enforcement for more efficient patrols (Plumptre et al., 2014). We concur with these findings, but highlight the need to account for imperfect detection and uneven sampling while developing threat maps to identify areas experiencing high poaching-related threats.

More efficient ranger patrols will undoubtedly deter poaching-related threats and may lead to apprehension of poachers. However, efficient prosecution of poachers when apprehended is also crucial for increasing the morale of rangers, encouraging them to continue performing their duties at the highest levels, and to discourage potential poachers from engaging in illegal activities within the park. Additionally, integrated conservation and development projects (Brandon et al., 1998; McShane & Wells, 2004), community-based conservation (Child, 1996; Gibson & Marks, 1995; Steinmetz, Srirattanaporn, Mor-Tip, & Seuaturien, 2014), payment for ecosystem services (Engel, Pagiola, & Wunder, 2008; Wunder, 2006) or alternative livelihood projects (Wright et al., 2016) are also crucial, as they seek to involve the local community in the conservation of protected areas through various means. These approaches could be instrumental in areas with high levels of poverty such as Rwanda, because they provide local villagers with an alternative to illegal activities (Milder, Scherr, & Bracer, 2010; Pagiola, Arcenas, & Platais, 2005). For example, preliminary results of experimental employment of ex-poachers to patrol with park rangers has resulted in an increased detection of poaching-related activities in NNP, while simultaneously providing an alternative income source to incentivize reduction of poaching from villagers outside of the park (M. K. Masozera, pers. comm.). This type of management scheme has been suggested as a way to reduce poaching threats elsewhere (Cooney, 2016; Wilkie, Painter, & Jacob, 2016), but its effectiveness remains untested.

By applying dynamic occupancy models to RBM data, we were able to estimate the occurrence of poaching-related threats within NNP, as well as identify factors influencing the spatial and temporal patterns of these threats, while accounting for imperfect detection and uneven sampling over the study period. This is one of the first studies to objectively evaluate poaching threats and to show that they can be reduced or eradicated by spatially targeting areas with high occurrence of threats and carefully planning and deploying ranger patrols to those sites. Using models of threat dynamics as a function of management actions such as this is rare, but such models are the basis for serious management efforts that are based on decision theory (e.g. Williams et al., 2002). These types of models enable park managers to objectively select management actions to meet conservation objectives. Our findings support the hypothesis that ranger patrols deter poaching-related activities within protected areas, which is a management action that, when combined with spatial and temporal data on poaching-related threats, could be incorporated into law enforcement protocols in the future. In addition, we show the importance of ranger posts in deterring illegal poaching activity; the threat map can be used as a guide to identify locations where additional posts can be established to reduce poaching-related threats. Finally, our results highlight the need for adequately modelling detection probability while quantifying anthropogenic threats, especially in dense forests and other areas, where illegal human activities could be easily missed by researchers and rangers. Without accounting for imperfect detection, we would have incorrectly concluded that poaching threats increased over our study period, when in fact the overall distribution of poaching threats had declined.

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AUTHORS' CONTRIBUTIONS

F.M., M.K.M and E.T. collected the data; J.F.M, J.D.N., J.E.H. and M.K.O. analysed the data; J.F.M., J.D.N. and M.K.O. conceived the study and wrote the manuscript. All authors contributed critically to the drafts and gave final approval for publication.

DATA ACCESSIBILITY

Data are available from the University of Florida Digital Archive: http://ufdc.ufl.edu//IR00009981/00001 (Moore et al., 2017).

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