

# Response of large galliforms and tinamous (Cracidae, Phasianidae, Tinamidae) to habitat loss and fragmentation in northern Guatemala

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**Abstract** The potential conservation value of fragmented or countryside landscapes in the tropics is being increasingly recognized. However, the degree to which fragmented landscapes can support species and the key patch and landscape features that promote population persistence remain poorly understood for elusive species such as ground-dwelling birds. We examined the presence/absence of seven species of galliforms and tinamous in 50 forest patches of 2.9–445 ha in northern Guatemala using camera traps and audiovisual surveying. After accounting for differences in detectability among species we found great variation in patterns of vulnerability of these species to habitat loss and fragmentation, with the three largest species being the most vulnerable. Distribution patterns of species among patches was influenced more strongly by measures of landscape context, such as the amount and configuration of habitat in the surrounding landscape, than within-patch variation in vegetation structure or disturbance. Our results indicate that large-bodied game birds may be particularly sensitive to habitat loss and fragmentation and emphasize that management efforts for these species need to go beyond consideration of local, within-patch factors to consider the impact of processes in the surrounding landscape. Our findings also demonstrate the utility of camera traps as a methodology for surveying large terrestrial bird species in fragmented landscapes.

**Keywords** Cracid, detectability, fragmentation, galliform, Guatemala, patch occupancy, Tinamiformes, vulnerability

## Introduction

Clearing of tropical forest for food production and urban expansion is proceeding at a tremendous rate (Asner et al., 2009), resulting in landscapes that contain small patches of forest surrounded by a matrix of agriculture, cattle pasture and urban lands. Variation exists in the ability

of species to use forest patches embedded in human-dominated environments, with some species being much more likely than others to persist within fragmented landscapes (Laurance, 1991, 2002; Gascon et al., 1999). The identification of which species are most at risk and the characteristics of patches and landscapes that influence the likelihood of persistence within fragmented environments are key conservation issues that need to be resolved for planning effective conservation strategies.

Previous research has shown that large terrestrial and/or game species such as galliforms are vulnerable to hunting pressure and habitat disturbance (Thiollay, 1999, 2005) and may disappear or become rare in single isolated forest remnants (Robinson, 1999). However, beyond interview-based occupancy research (Urquiza-Haas et al., 2009) little work has focused on understanding the factors influencing distribution of these species across large, highly fragmented landscapes. Given the site-specific nature of the response of birds to fragmentation (Sigel et al., 2010) more data from a variety of systems are needed to understand better how these species cope with environmental change. Because large birds such as cracids and tinamous often constitute a substantial portion of avian biomass in undisturbed neotropical forests (Terborgh et al., 1990; Robinson et al., 2000) and play important roles as seed predators and seed dispersers (Brooks & Strahl, 2000; Érard et al., 2007; Bertsch & Barreto, 2008b) their ability to persist within fragmented landscapes may have ramifications for the long-term trajectory of bird communities and forest composition within forest remnants.

In addition to traditional survey methods camera traps provide another methodology for documenting large-scale distribution patterns of terrestrial birds (O'Brien & Kinnaird, 2008). Although camera traps have been used primarily to document the presence or abundance of elusive terrestrial mammals (e.g. Maffei et al., 2004; Dillon & Kelly, 2008; Thornton et al., 2011a) they can also provide a wealth of information on the occupancy of large ground-dwelling birds, even when those species are not the focal subject of a particular study (O'Brien & Kinnaird, 2008). To date, however, the use of camera traps in this regard has been limited (O'Brien & Kinnaird, 2008).

We studied the response of three cracids (great curassow *Crax rubra*, crested guan *Penelope purpurascens*, plain chachalaca *Ortalis vetula*), ocellated turkey *Meleagris ocellata* and three tinamous (great tinamou *Tinamus*

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major, slaty-breasted tinamou *Crypturellus boucardi*, little tinamou *Crypturellus soui*) to forest loss and fragmentation in northern Guatemala by examining occupancy patterns of these species in forest patches. We assessed the vulnerability of these species to habitat loss and fragmentation and investigated the influence of patch- and landscape-level factors on distribution patterns of species among forest patches.

## Study area

We conducted this study on a 250,000-ha area in the Petén region of northern Guatemala (Fig. 1). The northernmost part of the study area is located within the buffer zone of the Maya Biosphere Reserve (a UNESCO world heritage site and the central section of the largest contiguous tropical forest in Central America) and the remainder on private lands further to the south. This area was a formerly contiguous forest but now consists of a diverse mosaic of land-use types (V.H. Ramos, pers. comm.). Forest cover in this area consists primarily of subtropical humid rainforest interspersed with scattered small patches of seasonally inundated *bajo* forest. Mean temperature in this region is 21–24 °C and mean annual precipitation 1,350 mm, with a marked dry season from late December to May when mean monthly rainfall is only 60 mm.

## Methods

### Site selection

Our study sites were 50 primary rainforest patches (hereafter focal patches) of 2.9–445.5 ha (mean  $68.5 \pm \text{SE } 98.7$  ha). We did not sample rainforest patches that were severely degraded by logging or fire (loss of > 25% canopy cover) but almost all patches included in the study were lightly degraded. Because of the size of our overall study area and difficulty of travel in certain areas we did not select patches randomly across the entire study landscape. Instead, we divided the area into five zones that contained multiple patches and surveyed the zones in a random order. Within each zone we randomly selected patches for study until a maximum of 15 patches had been surveyed.

### Occupancy surveys

We used camera trapping and audiovisual surveys to detect bird species within each patch. Sampling was from January to mid September. Mid-late wet season sampling (mid September to December) was avoided because of problems with camera-trap performance. Camera traps were set to survey for mid- to large-sized mammals (Thornton et al.,

2011a) but also recorded the presence of all seven bird species considered here. We placed cameras along roads and small and large game trails, and at water holes and in other areas containing substantial signs of use by animals. Although the proportion of cameras placed at each of these sites varied among patches, each patch had at least one camera placed at each type of site. We placed more cameras in larger patches: seven cameras in patches < 10 ha, 10 in patches  $\geq 10$  and < 20 ha, 14 in patches  $\geq 20$  and < 40 ha, 17 in patches  $\geq 40$  and < 80 ha, 20 in patches  $\geq 80$  and < 160 ha, 25 in patches  $\geq 160$  and < 320 ha, and 28 in patches  $\geq 320$  ha. We placed camera traps at least 10 m from the edge of patches, with the sensor c. 10–20 cm off the ground so that smaller species could not avoid detection by walking under the sensor. We used the following minimum spatial separation between cameras so that we would cover a greater area in larger patches: 50 m for patches < 20 ha, 100 m for patches < 80 ha, and 150 m for all other patches. Cameras were located in an approximate grid formation, with the caveat that we sought out the best locations possible for placement of each camera. We could typically survey 1–3 patches simultaneously (depending on patch size), using 30–40 cameras during each sample period.

We deployed camera traps for a 16-day period in each patch. A photograph of a particular species at any of the cameras within a patch was considered an indication of presence. We recorded presence/absence for each species within each patch after every 4-day interval. By dividing the 16-day period into 4-day sessions we created a series of repeat detection/non-detection data (i.e. a detection history) for use in modelling detection probabilities for each species (MacKenzie et al., 2006).

We also surveyed patches using audiovisual surveys in the early morning (between sunrise and 3 hours after sunrise), recording bird sightings and vocalizations. We acknowledge that the timing of surveys may not have been ideal for our study species, which are most vocal pre-dawn (Terborgh et al., 1990). However, as the overall aim of the audiovisual surveys was to document a wide range of primarily diurnal/crepuscular birds and mammals (Thornton et al., 2011a) we chose this timing as most appropriate. We sampled a subset ( $n = 17$ ) of patches in pre-dawn hours but, because of the low numbers of birds or mammals detected, these surveys were not continued and are not included in the analysis.

Audiovisual surveys were repeated five times within a 2-week period for each patch, resulting in a series of detection/non-detection data. Surveys were not performed in the rain because of low detectability in such conditions. Because we were recording the presence (not density) of species we did not cut transects but rather sought to walk through as much of the patch as possible to increase detection probabilities. We surveyed patches by walking

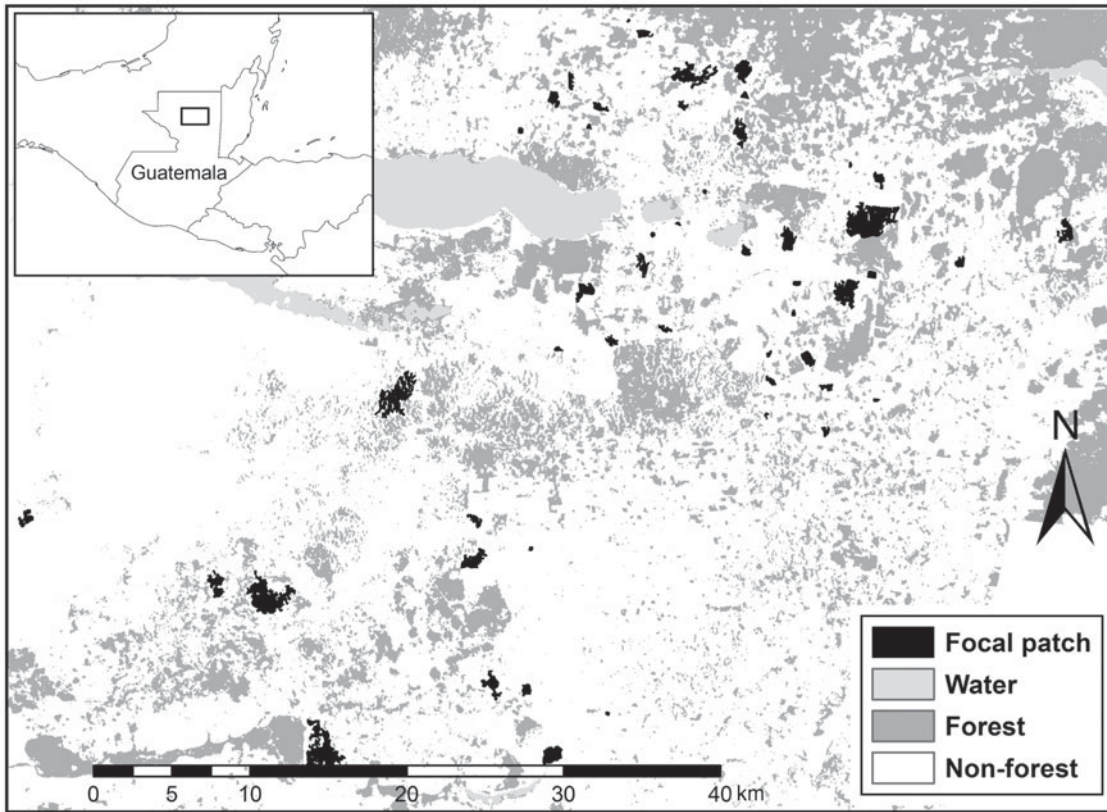


Fig. 1 Location of the 50 sampled patches within the study area (Thornton et al., 201b). Inset shows approximate location of the main map in northern Guatemala.

along small roads, footpaths and game trails, and by walking through sections without any obvious trails. We walked at c. 1 km per hour and recorded direct observations of animals and vocalizations as indications of presence within the patch. For patches < 10 ha we were able to walk through most or all of the patch in each session, with a new randomly chosen starting point for each survey. For patches too large to survey completely in one session we divided the site into 2–4 sections and randomly chose a section, a starting point and a compass direction for each session. We attempted to follow compass directions as closely as possible given the terrain, availability of trails and degree of understorey cover. We repeated this process until we had five surveys for the patch. The total distance walked over the five visits within each patch varied positively with patch size: 4 km walked within sites < 10 ha, 5 km within sites  $\geq 10$  and < 40 ha, 7.5 km within sites  $\geq 40$  and < 80 ha, 9 km within sites  $\geq 80$  and < 160 ha, and 10 km within sites  $\geq 160$  ha. We did not sample patches concurrently with cameras and audiovisual surveys because of concerns that our presence within patches would bias detections on cameras. For most patches we performed audiovisual surveys either 2 weeks before or 2 weeks after camera trapping. However, for a small subset of patches > 1 month elapsed between camera trapping and audiovisual surveys because of weather, access and other logistical problems.

#### Habitat measurements: patch variables

For each focal patch we calculated focal patch size and several indices of within-patch structure and disturbance (Table 1). We estimated the basal area of trees using the point-centred quarter method (PCQM; Cottom et al., 1953) along randomly placed transects within each focal patch. In each quadrat of the PCQM sample we recorded distance to the nearest stem in two size classes: 0–10 cm diameter at breast height (DBH) and  $\geq 10$  cm DBH. We also assessed evidence for past fire along the edge and interior of the patch and created a binary variable with 0 = no fire effects and 1 = fire along edge and/or < 25% of interior. We assessed cattle disturbance in the patches in an informal manner by noting observations of cattle, cattle paths, dung and tracks, and created a binary variable with 0 = cattle not recently present within the patch and 1 = cattle recently present.

#### Habitat measurements: landscape context

We created a vegetation map by performing an unsupervised classification of 2003 Landsat Enhanced Thematic Mapper Plus (ETM+) images with *ERDAS Imagine v. 9.0* (Leica Geosystems, Atlanta, USA) that identified four classes: water, pasture/agriculture, regenerating forest  $\leq 15$  years old, and primary forest/regenerating forest > 15 years

TABLE 1 Patch and landscape variables for the 50 focal patches in the study area in northern Guatemala (Fig. 1).

Variable	Mean $\pm$ SE	Description
<b>Patch</b>		
Focal patch size	68.5 $\pm$ 98.7	Area of focal forest patch (ha)
Basal area of large trees	20.0 $\pm$ 10.1	Basal area per ha of all large trees within the patch (stems $\geq$ 10 cm DBH)
Basal area of small trees/saplings	2.9 $\pm$ 1.2	Basal area per ha of all small trees/saplings within the patch (stems < 10 cm DBH)
Fire	0.42*	Evidence of fire within patch (binary)
Cattle	0.28*	Presence/absence of cattle in fragment (binary)
<b>Landscape</b>		
Proportion of forest	0.2 $\pm$ 0.1	Proportion of primary and secondary forest ( $\geq$ 15 years regrowth)
Proportion of regenerating forest	0.3 $\pm$ 0.1	Proportion of regenerating forest (< 15 years regrowth)
Density of patches	2.6 $\pm$ 0.9	Density of forest patches ( $\text{km}^{-2}$ )
Distance to nearest community	2.8 $\pm$ 1.6	Distance of the focal patch to the nearest human community (km)
Distance to reserve boundary	20.3 $\pm$ 11.6	Distance of the focal patch to the boundary of the Maya Biosphere (km)

\*Proportion of patches with evidence of fire or cattle disturbance

old. Primary forest and older regenerating forest were combined into one class because of our inability to separate these classes with Landsat imagery. The overall classification accuracy was 80.3%.

We measured landscape variables within 2-km buffers from the edge of focal patches and used *FRAGSTATS* (McGarigal et al., 2002) to calculate measures of habitat amount and configuration (Table 1). Proportion of forest in the landscape represented habitat amount, and we chose density of patches as our measure of habitat configuration because it was easily interpretable as an index of fragmentation and was not correlated with proportion of forest. We also calculated proportion of regenerating forest as a measure of low quality habitat around patches (Table 1).

We calculated two other metrics reflecting the landscape context of focal patches (Table 1). We calculated distance from the focal patch to the nearest continuous forest site > 10,000 ha (i.e. the Maya Biosphere Reserve boundary) as a measure of the potential effect of a nearby source, and distance from the focal patch to the nearest human community as a measure of hunting pressure and/or human disturbance. Finally, we determined the season of

sampling (dry vs early wet) for each patch. Correlation coefficients between all continuous potential predictor variables included in the analysis (patch, landscape, and additional variables) were < 0.5.

### Data analysis

We used detection/non-detection data from the 50 focal forest patches to model patch occupancy and detection probabilities with *PRESENCE v. 2.0* (Hines, 2006). Based on very limited data from our study species and closely related species we cannot rule out the possibility that some of the larger species may have had home ranges not completely enclosed by the sampling units, or were capable of moving between forest patches (Poulsen, 1994; Gonzalez et al., 1998; Bertsch & Barreto, 2008a). The occupancy estimator is therefore best interpreted as probability of use of a patch rather than probability of occupancy, and the detection parameter is best interpreted as a combination of two components: the probability that the species was within the patch when sampling occurred and the probability the species was detected, given it was within the patch (MacKenzie et al., 2006). For ease of presentation we use traditional occupancy terminology.

For six of the seven species we modelled the influence of covariates on detection and occupancy probability. We excluded ocellated turkeys from an analysis of covariate influence because of sparse data (detected in only two patches). However, we did develop a model for ocellated turkeys based on constant probabilities of detection and occupancy to obtain an estimate of proportion of patches occupied for this species. For the remaining species we first determined detection probabilities based on the camera-trapping and audiovisual survey data. The dataset that gave the higher overall detection probability was used in subsequent analyses. We did not combine data from cameras and audiovisual surveys for estimating occupancy and detection (multimethod occupancy modelling; Nichols et al., 2008) because camera trapping and audiovisual surveys were not conducted at the same time. We then modelled detection as a function of sampling effort (number of camera-trap nights or number of km walked) and season of survey, holding occupancy constant. The best-fit detection model for each species was determined using the corrected form of Akaike's Information Criterion adjusted for small sample sizes (AICc), which is appropriate when the sample size to parameter ratio is < 40 (Burnham & Anderson, 2002). This best-fit detection model was then used in all subsequent analyses of occupancy probabilities.

We tested a subset of 29 a priori occupancy models (Appendix) developed from the 11 patch and landscape variables. Candidate models included three models at the

TABLE 2 Estimates of detectability and proportion of patches occupied for the seven large terrestrial birds detected in our study.

Species	Mean probability of detection per survey	Naïve proportion of fragments occupied <sup>1</sup>	Corrected proportion of fragments occupied $\pm$ SE <sup>2</sup>
Great curassow <i>Crax rubra</i>	0.59	0.30	0.31 $\pm$ 0.08
Slaty-breasted tinamou <i>Crypturellus boucardi</i>	0.41	0.58	0.67 $\pm$ 0.10
Little tinamou <i>Crypturellus soui</i>	0.36	0.62	0.71 $\pm$ 0.14
Ocellated turkey <i>Meleagris ocellata</i>	0.50	0.04	0.04 $\pm$ 0.04
Plain chachalaca <i>Ortalis vetula</i>	0.44	0.78	0.83 $\pm$ 0.08
Crested guan <i>Penelope purpurascens</i>	0.22	0.12	0.19 $\pm$ 0.06
Great tinamou <i>Tinamus major</i>	0.40	0.46	0.52 $\pm$ 0.10

<sup>1</sup>Estimated proportion of patches occupied not corrected for detectability (number of fragments where species was detected at least once/total number of fragments)

<sup>2</sup>Estimated proportion of patches occupied corrected for detectability (sum of individual occupancy probabilities from each patch/total number of patches, based on parameter estimates from best-fit models)

patch level: focal patch size, focal patch structure (basal area of small trees/sapling and basal area of large trees), and focal patch disturbance (fire and cattle disturbance). Candidate models also included four models incorporating the effects of landscape context: habitat amount (percentage forest remaining in the buffer around focal patches), habitat configuration (density of forest patches in the buffer), matrix structure (percentage regenerating forest in the buffer), and distance effects (distance to nearest human community and distance to reserve boundary). We tested these patch and landscape models singly and also tested all possible combinations of two models considered simultaneously. We identified best-fit models and best-fit model sets (all models that fell within  $\Delta_4$  AICc values of the best-fit model) for each species. We did not test more complex models because of sample size limitations. Overall patch occupancy rates were calculated for each species and used as an index of vulnerability to habitat loss and fragmentation. Parameter estimates of covariate influence were calculated based on the best-fit models. For occupancy and detection covariates that appeared in more than one model in the

best-fit model sets we calculated model-averaged parameter estimates and unconditional standard errors (Burnham & Anderson, 2002). We assessed overdispersion in best-fit models for each species with a goodness-of-fit test procedure implemented in *PRESENCE* (MacKenzie & Bailey, 2004). We found no indications of overdispersion for any of the species.

Autocorrelation is problematic for classic statistical tests, such as regression, that rely on independently distributed errors and may lead to erroneous conclusions regarding the significance of covariates in studies of species–environment relationships (Lichstein et al., 2002). We therefore evaluated model residuals of our best-fit models in each analysis for evidence of spatial autocorrelation using Moran's *I* correlograms (Fortin & Dale, 2005). We used the following lag distances for calculation of Moran's *I*: 0–4, > 4–8, > 8–12, > 12–16 and > 16–20 km. A Monte Carlo randomization test with 999 permutations was used to determine the probability of obtaining an *I* value as large as the observed value in each lag category. Significance was tested using Bonferroni corrections, where the *i*th lag was tested at  $0.05/I$  (Fortin & Dale, 2005).

## Results

We obtained 521 photographs of the seven species of terrestrial birds in 12,963 camera-trap nights. We also obtained 850 photographs of 25 other bird species. More than half of these photographs were of two terrestrial ground doves (*Geotrygon montana* and *Leptotila verreauxi*). Detection probabilities varied among species (0.22–0.59; Table 2). Sampling effort influenced probability of detection for slaty-breasted tinamou, great tinamou and plain chachalacas. Detection probabilities were higher from camera trapping than for audiovisual surveys for great curassow, great tinamou, slaty-breasted tinamou and ocellated turkey, and vice versa for crested guan, little tinamou and plain chachalaca.

Species displayed large differences in the proportion of patches occupied (Table 2). Great curassow, crested guan, ocellated turkey and great tinamou had low overall patch occupancy rates. By contrast, the slaty-breasted tinamou, little tinamou and plain chachalaca had relatively high rates of patch occupancy (Table 2).

Species responded strongly to a variety of covariates. Best-fit models had very high AIC weights ( $> 0.5$ ) for five of the six species, indicating low model selection uncertainty for the set of models tested (Table 3). Plain chachalaca was the only species with a high degree of model selection uncertainty and also the only species where the null model was within  $\Delta_4$  AICc values of the best-fit model. Based on parameter estimates from best-fit model sets greater amounts of habitat in the landscape surrounding patches

TABLE 3 Patch occupancy models for galliforms and tinamous. All models that fall within  $\Delta_4$  AICc units of the best-fit model are shown (except for chachalacas where only models within  $\Delta_2$  AICc values of best-fit models are shown because of the large number of models within  $\Delta_4$  AICc values).

Model <sup>1</sup>	$K^2$	$\log(L)^3$	AICc	$\Delta$ AICc	$w^4$
<b>Great curassow</b>					
P(.) $\psi$ (PF + DISTC + DISTS)	5	-62.96	137.27	0.00	0.66
P(.) $\psi$ (FPS + DISTC + DISTS)	5	-64.53	140.41	3.14	0.14
<b>Slaty-breasted tinamou</b>					
P(effort) $\psi$ (FPS + PREG)	5	-93.63	198.61	0.00	0.55
P(effort) $\psi$ (FPS + PF)	5	-94.24	199.84	1.23	0.27
<b>Little tinamou</b>					
P(.) $\psi$ (PF + DISTC + DISTS)	5	-127.13	265.62	0.00	0.91
<b>Plain chachalaca</b>					
P(effort) $\psi$ (DFP)	4	-156.68	322.25	0.00	0.10
P(effort) $\psi$ (.)	3	-157.89	322.29	0.04	0.10
P(effort) $\psi$ (PREG + DISTC + DISTS)	6	-154.30	322.55	0.30	0.09
P(effort) $\psi$ (DISTC + DISTS)	5	-155.70	322.76	0.51	0.08
P(effort) $\psi$ (PF)	4	-156.97	322.83	0.56	0.08
P(effort) $\psi$ (FPS + PF)	5	-155.92	323.20	0.95	0.06
P(effort) $\psi$ (FPS)	4	-157.22	323.32	1.08	0.06
P(effort) $\psi$ (PF + DISTC + DISTS)	6	-154.85	323.64	1.39	0.05
P(effort) $\psi$ (DFP + DISTC + DISTS)	6	-154.85	323.70	1.45	0.05
P(effort) $\psi$ (FPS + DFP)	5	-156.20	323.76	1.50	0.05
<b>Crested guan</b>					
P(.) $\psi$ (FPS + DFP)	4	-25.93	60.76	0.00	0.92
<b>Great tinamou</b>					
P(effort) $\psi$ (FPS + DFP)	5	-77.51	166.38	0.00	0.74

<sup>1</sup>P, Probability of detection;  $\psi$ , probability of occupancy. Explanatory variables are: effort, sampling effort in patch; FPS, size of the sampled patch; PF, proportion of forest in the landscape (i.e. habitat amount); DFP, density of forest patches in the landscape (i.e. habitat configuration); PREG, proportion of regenerating forest in the landscape; DISTC, distance to nearest human community; DISTS, distance to boundary of the Maya Biosphere Reserve

<sup>2</sup>Number of parameters in the model

<sup>3</sup>Maximized log-likelihood

<sup>4</sup>Model weights

increased occupancy probabilities for two species (great curassow and little tinamou; Table 4). A greater density of forest patches in the landscape surrounding patches decreased occupancy probabilities of great tinamou and crested guan. Although density of forest patches increased occupancy probabilities of plain chachalaca, unconditional standard errors were larger than model-averaged parameter estimates, suggesting that this variable had a weak effect on occupancy. Similarly, although proportion of regenerating forest in the landscape appeared in the best-fit model for slaty-breasted tinamous, the standard error was high relative to the parameter estimate. Larger focal patch size was associated with increasing rates of occupancy for three species (great tinamou, crested guan and slaty-breasted tinamou; Table 4). Increasing distance to the nearest human community decreased occupancy of little tinamou and increased occupancy of great curassows. Increasing distance to source increased occupancy of both little tinamou and great curassows. We did not find evidence of significant autocorrelation in the residuals of best-fit models for any of the species.

## Discussion

The four largest species in our study (great curassow, crested guan, ocellated turkey and great tinamou) were the least common in forest patches and therefore the most vulnerable to forest loss and fragmentation. By contrast the three smallest species (little tinamou, slaty-breasted tinamou and plain chachalaca) were the least vulnerable and occupied over half of the surveyed patches. Although patterns of relative use of patches may be misleading, as certain species may naturally be more rare and therefore occupy fewer patches (i.e. the problem of passive sampling effects), a subsidiary analysis correcting for these effects by comparing occupancy probabilities of forest patches with continuous forest sites confirmed our results (D. Thornton, unpubl. data). Patch occupancy patterns of almost all species in our study were influenced strongly by measures of landscape context, with relatively little influence of habitat structure or disturbance within patches. Focal patch size also exerted the expected strong positive influence on occupancy patterns.

TABLE 4 Parameter estimates ( $\pm$  SE) for all explanatory variables that appeared in best-fit model sets. For variables that appeared in more than one model within the best-fit model set for a single species, the values shown are model-averaged parameter estimates and unconditional standard errors.

Species	Sampling effort in patch (trap-nights or km walked)	Sampled patch size (ha)	Proportion of forest	Density of forest patches ( $\text{km}^{-2}$ )	Proportion of regenerating forest	Distance to nearest human community (km)	Distance to boundary (km)
Great curassow		$0.88 \pm 0.40$	$1.53 \pm 0.67$			$0.63 \pm 0.40$	$1.54 \pm 0.72$
Slaty-breasted tinamou	$0.78 \pm 0.31$	$5.88 \pm 4.11$	$2.64 \pm 1.50$		$9.4 \pm 9.9$		
Little tinamou			$1.83 \pm 0.72$			$-0.81 \pm 0.48$	$1.6 \pm 0.73$
Crested guan		$5.44 \pm 3.41$		$-5.81 \pm 3.61$			
Plain chachalaca	$-0.30 \pm 0.18$	$-0.72 \pm 0.66$	$0.99 \pm 1.18$	$0.92 \pm 1.12$	$1.05 \pm 0.82$	$-1.25 \pm 1.46$	$-0.86 \pm 0.85$
Great tinamou	$0.59 \pm 0.23$	$10.0 \pm 6.01$		$-1.8 \pm 0.98$			

Patterns in relative vulnerability of the studied species to habitat loss and fragmentation largely agree with interview-based occupancy surveys in the nearby Yucatán (Urquiza-Haas et al., 2009). Larger species in the Yucatán study (great curassows, crested guan, great tinamous and ocellated turkeys) had lower occupancy rates than the smaller tinamous or plain chachalaca. Although little additional work detailing patch occupancy rates of our study species or their close relatives has been published, large galliforms and tinamous are often rare or absent in isolated forest remnants (e.g. Robinson, 1999; Pearson et al., 2009; Manica et al., 2010). In addition to large body size, which is often implicated as being closely associated with vulnerability to fragmentation in tropical birds (Kattan et al., 1994; Lees & Peres, 2010), these species share other traits that are often associated with vulnerability in neotropical avian species, such as a frugivore–granivore diet and forest dependency (Vetter et al., 2011). These species are also often heavily hunted, which can increase vulnerability in fragmented landscapes (Peres, 2001).

The strong negative effect of habitat configuration (density of forest patches) on crested guans and great tinamous suggests that more fragmented landscapes are less suitable for these species. The response of these two species contrasts with many studies of temperate bird fauna, which have almost universally shown that habitat configuration has relatively weak effects on species distribution and abundance patterns compared with the influence of habitat area (Fahrig, 2003; Smith et al., 2009), but is consistent with other recent work on tropical birds (Cerezo et al., 2010). A negative response to increasingly fragmented habitat, holding habitat amount constant, could be driven by sensitivity to edges as more fragmented habitats tend to have a higher density of edges. Tropical birds respond strongly to edges (Laurance et al., 2002; Lindell et al., 2007) and may be more likely to respond in a negative manner to edges than temperate species because of factors such as a shorter history of exposure to patchiness, narrower resource requirements, or other factors (Lindell et al., 2007).

The relative influence of habitat amount vs configuration on tropical bird species should be further examined on multiple large and independent landscapes as our study evaluated these factors only in the neighbourhood around patches (a patch–landscape study sensu McGarigal & Cushman, 2002).

The positive effect of the amount of habitat in the landscape and also of focal patch size on occupancy patterns is consistent with many other studies of bird response to fragmentation (e.g. Winter et al., 2006; Evans et al., 2009) and may be driven by positive responses to increasing habitat area or avoidance of edges (Reino et al., 2009). The differential effect of distance to human community on species in our study adds to recent work showing that human disturbance can exert a strong impact on occupancy patterns of avian species in fragmented neotropical habitats, independent of landscape structure (Urquiza-Haas et al., 2009; Aubad et al., 2010). Patches closer to human habitations are often used more frequently for hunting (Parry et al., 2009) and experience higher levels of other forms of human disturbance (e.g. collection of firewood; Aubad et al., 2010).

The general lack of response by species in our study to within-patch vegetation structure or disturbance is counter to many studies of tropical bird species that find an effect of patch quality on distribution patterns among patches (e.g. Lees & Peres, 2010). This finding may indicate a greater sensitivity of these large-bodied species to coarse-grained landscape factors rather than fine-grained within-patch factors, or that the within-patch factors we measured do not adequately represent patch quality for our species. Our exclusion of heavily disturbed patches from analysis, as well as our binary (instead of continuous) measures of cattle and fire disturbance, may have also contributed to a lack of effect of within-patch variables on occupancy patterns.

### Conclusions and management recommendations

In our study large terrestrial species were highly vulnerable to habitat loss and fragmentation in northern Guatemala.

Because we were able to incorporate detectability in our analysis, our findings do not reflect detection differences among species but instead depict real patterns in vulnerability. Although none of the species that showed a marked negative response are currently considered threatened, all three species are declining across their range, with the great curassow categorized as Vulnerable and the ocellated turkey as Near Threatened on the IUCN Red List (IUCN, 2011). Significantly, deforestation in our study area began only 30–40 years ago yet this was ample time to see substantial declines in occupancy of the study species. Synergistic effects of reduced habitat area and increased hunting pressure could quickly drive the decline of these and similar large-bodied species in fragmented landscapes (Peres, 2001). Research to separate effects of hunting pressure vs landscape conversion on large bird species may be useful to identify the most effective management options for such species in human-dominated landscapes.

The strong response of our study species to landscape context emphasizes the importance of management efforts that go beyond consideration of local factors such as patch size or structure (Villard et al., 1999). Consideration of the surrounding landscape may be particularly important for highly vagile/large-bodied species such as those in our study. The strong response to habitat configuration suggests that, in addition to preserving sufficient amounts of habitat, increased attention to management of landscape pattern may be necessary to preserve tropical bird species. This could take the form of conservation planning in conjunction with outreach efforts to landowners (e.g. Thomson et al., 2009) to maintain forest cohesion across the landscape.

To date camera trapping has been an underutilized methodology for surveying bird species (O'Brien & Kinnaird, 2008). Our findings demonstrate that this methodology provides a complement to audiovisual surveys and results in relatively high detection rates for large terrestrial species. Our success at photo-capturing terrestrial birds may be related to the fact that we placed cameras at relatively low heights (10–20 cm) off the ground so that smaller animals would not escape detection. Significantly, this methodology did not affect our ability to detect larger mammals, although it would have affected our ability to individually identify larger mammals had this been a goal of our study. We support the recommendation of O'Brien & Kinnaird (2008) that camera trapping provides an effective means to estimate occupancy parameters for elusive terrestrial bird species.

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## References

- ASNER, G.P., RUDEL, T.K., AIDE, T.M., DEFRIES, R. & EMERSON, R. (2009) A contemporary assessment of change in humid tropical forests. *Conservation Biology*, 23, 1386–1395.
- AUBAD, J., ARAGON, P. & RODRIGUEZ, M.A. (2010) Human access and landscape structure effects on Andean forest bird richness. *Acta Oecologia*, 36, 396–402.
- BERTSCH, C. & BARRETO, G.R. (2008a) Abundance and home range of the yellow-knobbed curassow (*Crax daubentoni*) in the Venezuelan central llanos. *Ornitología Neotropical*, 19, 287–293.
- BERTSCH, C. & BARRETO, G.R. (2008b) Diet of the yellow-knobbed curassow in the central Venezuelan llanos. *The Wilson Journal of Ornithology*, 120, 767–777.
- BROOKS, D.M. & STRAHL, S.D. (2000) *Curassows, Guans, and Chachalacas: Status Survey and Conservation Action Plan for Cracids 2000–2004*. IUCN/Species Survival Commission Cracid Specialist Group, Gland, Switzerland.
- BURNHAM, K. & ANDERSON, D. (2002) *Model Selection and Multimodel Inference*. Springer-Verlag, New York, USA.
- CEREZO, A., PERELMAN, S. & ROBBINS, C.S. (2010) Landscape-level impact of tropical forest loss and fragmentation on bird occurrence in eastern Guatemala. *Ecological Modelling*, 221, 512–526.
- COTTOM, G., CURTIS, J.T. & HALE, B.W. (1953) Some sampling characteristics of a population of randomly dispersed individuals. *Ecology*, 34, 741–757.
- DILLON, A. & KELLY, M.J. (2008) Ocelot home range, overlap and density: comparing radio telemetry with camera trapping. *Journal of Zoology*, 275, 391–398.
- ÉRARD, C., THÉRY, M. & SABATIER, D. (2007) Fruit characters in the diet of syntopic large frugivorous forest bird species in French Guiana. *Revue D'Ecologie–La Terre Et La Vie*, 62, 323–350.
- EVANS, K.L., NEWSON, S.E. & GASTON, K.J. (2009) Habitat influences on urban avian assemblages. *Ibis*, 151, 19–39.
- FAHRIG, L. (2003) Effects of habitat fragmentation on biodiversity. *Annual Review of Ecology, Evolution, and Systematics*, 34, 487–515.
- FORTIN, M.-J. & DALE, M. (2005) *Spatial Analysis: A Guide for Ecologists*. Cambridge University Press, Cambridge, UK.
- GASCON, C., LOVEJOY, T.E., BIERREGAARD, R.O. JR, MALCOLM, J.R., STOUFFER, P.C., VASCONCELOS, H.L. et al. (1999) Matrix habitat and species richness in tropical forest remnants. *Biological Conservation*, 91, 223–229.
- GONZALEZ, M.J., QUIGLEY, H. & TAYLOR, A.C. (1998) Habitat use and reproductive ecology of the ocellated turkey in Tikal National Park, Guatemala. *The Wilson Bulletin*, 110, 505–510.
- HINES, J.E. (2006) *PRESENCE 2 – Software to Estimate Patch Occupancy and Related Parameters*. US Geological Service–Patuxent Wildlife Research Center. <http://www.mbr-pwrc.usgs.gov/software/presence.html> [accessed 29 March 2010].
- IUCN (2011) *IUCN Red List of Threatened Species v. 2011.2*. IUCN, Gland, Switzerland. <http://www.iucnredlist.org> [accessed 12 March 2012].



- KATTAN, G.H., ALVAREZLOPEZ, H. & GIRALDO, M. (1994) Forest fragmentation and bird extinctions: San Antonio eighty years later. *Conservation Biology*, 8, 138–146.
- LAURANCE, W.F. (1991) Ecological correlates of extinction proneness in Australian tropical rain forest mammals. *Conservation Biology*, 5, 79–89.
- LAURANCE, W.F. (2002) Hyperdynamism in fragmented habitats. *Journal of Vegetation Science*, 13, 595–602.
- LAURANCE, W.F., LOVEJOY, T.E., VASCONCELOS, H.L., BRUNA, E.M., DIDHAM, R.K., STOUFFER, P.C. et al. (2002) Ecosystem decay of Amazonian forest fragments: a 22-year investigation. *Conservation Biology*, 16, 605–618.
- LEES, A.C. & PERES, C.A. (2010) Habitat and life history determinants of antbird occurrence in variable-sized Amazonian forest fragments. *Biotropica*, 42, 614–621.
- LICHSTEIN, J.W., SIMONS, T.R., SHRINER, S.A. & FRANZREB, K.E. (2002) Spatial autocorrelation and autoregressive models in ecology. *Ecological Monographs*, 72, 445–463.
- LINDELL, C.A., RIFFELL, S.K., KAISER, S.A., BATTIN, A.L., SMITH, M.L. & SISK, T.D. (2007) Edge responses of tropical and temperate birds. *The Wilson Journal of Ornithology*, 119, 205–220.
- MACKENZIE, D.I. & BAILEY, L.L. (2004) Assessing the fit of site-occupancy models. *Journal of Agricultural, Biological, and Environmental Statistics*, 9, 300–318.
- MACKENZIE, D.I., NICHOLS, J.D., ROYLE, A.J., POLLOCK, K.H., BAILEY, L.L. & HINES, J.E. (2006) *Occupancy Estimation and Modeling: Inferring Patterns and Dynamics of Species Occurrence*. Elsevier, Boston, USA.
- MAFFEI, L., CUELLAR, E. & NOSS, A. (2004) One thousand jaguars (*Panthera onca*) in Bolivia's Chaco? Camera trapping in the Kaa-Iya National Park. *Journal of Zoology*, 262, 295–304.
- MANICA, L.T., TELLES, M. & DIAS, M. (2010) Bird richness and composition in a cerrado fragment in the state of São Paulo. *Brazilian Journal of Biology*, 70, 243–254.
- MCGARIGAL, K. & CUSHMAN, S.A. (2002) Comparative evaluation of experimental approaches to the study of habitat fragmentation effects. *Ecological Applications*, 12, 335–345.
- MCGARIGAL, K., CUSHMAN, S.A., NEEL, M.C. & ENE, E. (2002) FRAGSTATS: Spatial Pattern Analysis Program for Categorical Maps. <http://www.umass.edu/landeco/research/fragstats/fragstats.html> [accessed 13 March 2012].
- NICHOLS, J.D., BAILEY, L.L., O'CONNELL, A.F., TALANCY, N.W., GRANT, E.H.C., GILBERT, A.T. et al. (2008) Multi-scale occupancy estimation and modelling using multiple detection methods. *Journal of Applied Ecology*, 45, 1321–1329.
- O'BRIEN, T.G. & KINNAIRD, M.F. (2008) A picture is worth a thousand words: the application of camera trapping to the study of birds. *Bird Conservation International*, 18, S144–S162.
- PARRY, L., BARLOW, J. & PERES, C.A. (2009) Allocation of hunting effort by Amazonian smallholders: implications for conserving wildlife in mixed-use landscapes. *Biological Conservation*, 142, 1777–1786.
- PEARSON, D.L., ANDERSON, C.D., MITCHELL, B.R., ROSENBERG, M.S., NAVARRETE, R. & COOPMANS, P. (2009) Testing hypotheses of bird extinctions at Rio Palenque, Ecuador, with informal species lists. *Conservation Biology*, 24, 500–510.
- PERES, C.A. (2001) Synergistic effects of subsistence hunting and habitat fragmentation on Amazonian forest vertebrates. *Conservation Biology*, 15, 1490–1505.
- POULSEN, B.O. (1994) Movements of single birds and mixed-species flocks from isolated fragments of cloud forest in Ecuador. *Studies on Neotropical Fauna and Environment*, 29, 149–160.
- REINO, L., BEJA, P., OSBORNE, P.E., MORGADO, R., FABIAO, A. & ROTENBERRY, J.T. (2009) Distance to edges, edge contrast and landscape fragmentation: interactions affecting farmland birds around forest plantations. *Biological Conservation*, 142, 824–838.
- ROBINSON, J.G., BRAUN, J.D. & ROBINSON, S.K. (2000) Forest bird community structure in central Panama: influence of spatial scale and biogeography. *Ecological Monographs*, 70, 209–235.
- ROBINSON, W.D. (1999) Long-term changes in the avifauna of Barro Colorado Island, Panama, a tropical forest isolate. *Conservation Biology*, 13, 85–97.
- SIGEL, B.J., ROBINSON, W.D. & SHERRY, T.W. (2010) Comparing bird community responses to forest fragmentation in two lowland Central American reserves. *Biological Conservation*, 143, 340–350.
- SMITH, A.C., KOPER, N., FRANCIS, C.M. & FAHRIG, L. (2009) Confronting collinearity: comparing methods for disentangling the effects of habitat loss and fragmentation. *Landscape Ecology*, 24, 1271–1285.
- TERBORGH, J., ROBINSON, S.K., PARKER, III, T.A., MUNN, C.A. & PIERPONT, N. (1990) Structure and organization of an Amazonian forest bird community. *Ecological Monographs*, 60, 213–238.
- THIOLLAY, J.-M. (1999) Responses of an avian community to rain forest degradation. *Biodiversity and Conservation*, 8, 513–534.
- THIOLLAY, J.-M. (2005) Effects of hunting on Guianan forest game birds. *Biodiversity and Conservation*, 14, 1121–1135.
- THOMSON, J.R., MOILANEN, A.J., VESK, P.A., BENNETT, A.F. & MACNALLY, R. (2009) Where and when to revegetate: a quantitative method for scheduling landscape reconstruction. *Ecological Applications*, 19, 817–828.
- THORNTON, D.H., BRANCH, L.C. & SUNQUIST, M.E. (2011a) Passive sampling effects and landscape location alter associations between species traits and response to fragmentation. *Ecological Applications*, 21, 817–829.
- THORNTON, D.H., BRANCH, L.C. & SUNQUIST, M.E. (2011b) The relative influence of habitat loss and fragmentation: do tropical mammals meet the temperate paradigm? *Ecological Applications*, 21, 2324–2333.
- URQUIZA-HAAS, T., PERES, C.A. & DOLMAN, P.M. (2009) Regional scale effects of human density and forest disturbance on large-bodied vertebrates throughout the Yucatán Peninsula, Mexico. *Biological Conservation*, 142, 134–148.
- VETTER, D., HANSBAUER, M., VEGVARI, Z. & STORCH, I. (2011) Predictors of forest fragmentation sensitivity in Neotropical vertebrates: a quantitative review. *Ecography*, 34, 1–8.
- VILLARD, M.A., TRZCINSKI, M.K. & MERRIAM, G. (1999) Fragmentation effects on forest birds: relative influence of woodland cover and configuration on landscape occupancy. *Conservation Biology*, 13, 774–783.
- WINTER, M., JOHNSON, D.H., SHAFFER, J.A., DONOVAN, T.M. & SVEDARSKY, W.D. (2006) Patch size and landscape effects on density and nesting success of grassland birds. *Journal of Wildlife Management*, 70, 158–172.

## Biographical sketches

DANIEL THORNTON is interested in understanding the multiscaled response of species to landscape change and the application of distribution and occupancy modelling to the conservation of large vertebrates. LYN BRANCH has broad interests in the ecology and conservation of wildlife in Latin America, with a focus on impacts of landscape change on wildlife populations and synergisms between these processes and other anthropogenic factors that affect wildlife. MEL SUNQUIST has an interest in mammalian ecology and conservation, with a focus on how best to conserve carnivores in increasingly human-dominated landscapes.

APPENDIX The 29 occupancy models tested for each species. Note that these models were fit after a best-fit detection model was identified for each species, based on the sampling effort of covariates and season of survey.

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### Model\*

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null model  
 FPS  
 DFP  
 PF  
 PREG  
 CAT + FIRE  
 BALRG + BASM  
 DISTC + DISTC  
 FPS + PF  
 FPS + DENP  
 FPS + PREG  
 FPS + DISTC + DISTC  
 FPS + CAT + FIRE  
 FPS + BALRG + BASM  
 PF + DENP  
 PF + PREG  
 PF + CAT + FIRE  
 PF + BALRG + BASM  
 PF + DISTC + DISTC  
 DFP + PREG  
 DFP + CAT + FIRE  
 DFP + BALRG + BASM  
 DFP + DISTC + DISTC  
 PREG + BALRG + BASM  
 PREG + CAT + FIRE  
 PREG + DISTC + DISTC  
 CAT + FIRE + BALRG + BASM  
 CAT + FIRE + BALRG + BASM  
 BALRG + BASM + DISTC + DISTC

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\*FPS, size of the sampled patch; PF, proportion of forest in the landscape (i.e. habitat amount); DFP, density of forest patches in the landscape (i.e. habitat configuration); PREG, proportion of regenerating forest in the landscape; BALRG, basal area of large trees; BASM, basal area of small trees/saplings; CAT, presence of cattle within patch (binary); FIRE, indications of past fire within patch (binary); DISTC, distance to nearest human community; DISTC, distance to boundary of the Maya Biosphere Reserve