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Impact of habitat alteration on endemic Afromontane chameleons: evidence for historical population declines using hierarchical spatial modelling

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ABSTRACT

Aim We map estimated historical population declines resulting from species-specific models of sensitivity to habitat fragmentation for three forest-dependent chameleons.

Location East Usambara Mountains, Eastern Arc Mountains, Tanzania.

Methods We surveyed three chameleon species (*Rhampholeon spinosus*, *Rhampholeon temporalis* and *Trioceros deremensis*) along 32.2 km of transects and used a hierarchical, distance-sampling model to estimate densities. The model included habitat characteristics at the landscape (patch) and local (transect) scales while accounting for detectability. By analysing the model in a Bayesian framework, we were able to propagate error through the entire analysis and obtain exact solutions despite small sample sizes. We then used our estimated relationships between habitat and density to project chameleon population sizes across current and historical land cover maps of the study area (230 km^2), giving an estimate of the impact of anthropogenic habitat alteration on these species.

Results Species' densities increased in larger patches and further from patch edges and varied seasonally. Local vegetation characteristics had significant relationships with expected chameleon densities, though effect sizes were small. Estimates of total current population sizes varied by two orders of magnitude among species, but each was 49–79% higher than detection-naïve estimates. All three declined from estimated historical levels by approximately 60% in the study area, approximately one-third more than would be expected from forest loss alone. Remaining populations of the study species are predominantly located in protected nature reserves, so the future of these species will likely be determined by the degree of protection offered by the nature reserves.

Main conclusions Habitat loss and fragmentation have greatly reduced forest-dependent chameleon population sizes in the East Usambara Mountains. Populations of these species in other areas are experiencing higher rates of habitat loss. Efforts aimed at ensuring the efficacy of protected forests may be a key to conserving remaining populations.

Keywords

Chamaeleonidae, density–area relationship, distance sampling, edge effects, habitat fragmentation, hierarchical Bayesian model.

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INTRODUCTION

Habitat alteration is the greatest threat facing biodiversity (Vitousek, 1997; Vié *et al.*, 2009). Yet despite a long history of research (Haila, 2002; Laurance *et al.*, 2010), determining the effects of habitat alteration, especially fragmentation (Ewers & Didham, 2006), can be challenging. Two complicating factors are the effects of scale and the detectability of the study species. Studies investigating the effects of fragmentation on animals (e.g. Connor *et al.*, 2000; Watling & Donnelly, 2006) commonly consider habitat patches as their spatial resolution or grain, effectively assuming that patches are homogenous. However, patterns that appear at one level of organization may be caused by mechanisms operating at finer scales (Levin, 1992). For instance, the correlation between organism density and patch area may be driven by mechanisms acting at a finer scale, such as edge effects (Ewers & Didham, 2007). Not acknowledging the influence of factors operating at different scales can lead to erroneous conclusions. Although ecologists have long recognized these hierarchical relationships in biological systems (Johnson, 1980; Urban *et al.*, 1987; Kotliar & Wiens, 1990), the analytical methods to properly analyse these data are a more recent development (e.g. Mackey & Lindenmayer, 2001; Royle *et al.*, 2007). Another recent analytical development is the analysis of hierarchical data to account for detectability (Royle *et al.*, 2007). As the number of animals observed is a function of both abundance and detectability, specific methods are necessary to estimate total population sizes and account for spatial and temporal changes in detectability (Mazerolle *et al.*, 2007), which may influence estimates of population trends (e.g. Pfaller *et al.*, 2013). Methods to account for detectability are available for estimates of occupancy (Bailey *et al.*, 2007), richness (Dorazio *et al.*, 2011) and density/abundance (Thomas *et al.*, 2010).

Studies of reptiles are particularly susceptible to ignoring detectability (Mazerolle *et al.*, 2007); of the 22 studies of reptile responses to fragmentation that we reviewed, only two studies (Sarre, 1998; Hokit & Branch, 2003) of single lizard species explicitly accounted for detectability in density/abundance estimates. Studies that ignore detectability may still adequately estimate trends in abundance if detectability is constant across space and time, but they cannot accurately estimate absolute abundances. Given the relative paucity of reptile studies overall, accurate abundance estimates are valuable for theory and conservation. Reptiles are diverse (Pincheira-Donoso *et al.*, 2013), are one of the most threatened taxa globally (International Union for the Conservation of Nature (IUCN), 2012a; Böhm *et al.*, 2013) and may be particularly vulnerable to climate change (Huey *et al.*, 2009). Yet a recent meta-analysis of the impacts of habitat fragmentation on vertebrates found 730 applicable datasets on 552 species, with only 1% of the datasets on reptiles (Vetter *et al.*, 2011). Clearly, more reptile research is warranted, particularly studies that can generate robust population estimates.

We assessed multiscale effects of habitat fragmentation on a previously understudied taxa and region – chameleons in the Eastern Arc Mountains (EAM) of Tanzania – while explicitly incorporating detectability. The EAM are globally significant for their high diversity and endemicity (Rodgers & Homewood, 1982; Kingdon, 1990; Lovett, 1998; Myers *et al.*, 2000; Burgess *et al.*, 2007) and for the critical ecosystem services they provide (Fisher *et al.*, 2011). However, the mountains have lost ~ 80% of their historical forest, and the remaining forest is highly fragmented (Newmark, 1998; Hall *et al.*, 2009). Thus, understanding the impacts of habitat loss and fragmentation on EAM biodiversity is an urgent problem. Research on forest fragmentation in the EAM has focused on avifauna (Newmark, 1991; Cordeiro, 2005; Newmark & Stanley, 2011; Korfanta *et al.*, 2012), trees (Cordeiro & Howe, 2001; Cordeiro *et al.*, 2009) and small mammals (Stanley *et al.*, 2011), while herpetofauna have received little attention. The EAM support a unique and diverse herpetofauna (Spawls *et al.*, 2002; Harper *et al.*, 2010), including 22 endemic or nearly endemic chameleon species [~ 11% of global chameleon diversity (Tilbury, 2010)], most of which rely on forested habitat. Additionally, Tanzania is one of the largest chameleon exporters globally (Carpenter *et al.*, 2004), further threatening chameleon species. While recent research has increased understanding of EAM chameleon systematics (Mariaux & Tilbury, 2006; Mariaux *et al.*, 2008; Menegon *et al.*, 2009; Tilbury & Tolley, 2009), the ecology and conservation status of most species is unknown.

Our objective was to determine the relationship between landscape characteristics and chameleon population densities in order to estimate population sizes. We used a hierarchical, distance-sampling model that accounted for detectability and estimated relationships between habitat covariates and expected chameleon density at multiple spatial scales. Covariates at the patch scale included forest patch area and between-patch distance (i.e. isolation); local (transect) scale covariates included distance to patch edge and various metrics of vegetation cover. We used this model to extrapolate chameleon densities across the East Usambara Mountain plateau based on current and historical landscape configuration. Comparison of estimated population sizes across the time periods allowed us to assess the impact of anthropogenic habitat alteration (Ewers *et al.*, 2010).

METHODS

Location and study species

The East Usambara Mountains are part of Tanzania's Eastern Arc Mountain biodiversity hotspot (Myers *et al.*, 2000). Archaeological evidence suggests that humans have inhabited the Eastern Arc Mountains for 2000 years (Soper, 1967; Schmidt, 1989). Sediment cores indicate that this expansion of human populations coincided with forest degradation (Mumbi *et al.*, 2008; Heckmann *et al.*, 2014) in the otherwise stable Eastern Arc forests (Fjeldsaå & Lovett, 1997;

Mumbi *et al.*, 2008; Finch *et al.*, 2009), which fits the timeframe of anthropogenic influence in nearby mountainous areas (Jolly *et al.*, 1997; Marchant & Taylor, 1998; Vincens *et al.*, 2003). Vestigial forest patches throughout the Eastern Arc Mountains suggest that forest was nearly continuous prior to anthropogenic influence (Newmark, 2002) – a widely made assumption (e.g. Newmark, 1998, 2002; FBD, 2006; Burgess *et al.*, 2007; Finch *et al.*, 2009; Hall *et al.*, 2009). Forest cover remained extensive until European settlement at the end of the 19th century (Conte, 2004; FBD, 2006; Hall *et al.*, 2009). However, as of 2000, only 32% (263 km^2 of 714 km^2) remained forested (Hall *et al.*, 2009). This remaining forest is heavily fragmented by tea plantations, eucalyptus groves and small-scale farming. The 12 forest patches surveyed in this study ranged in area from 0.95 to 722 ha and in between-patch distance from 10 to 1742 m (Table 1). Several of these forest patches were previously described by Newmark (Newmark, 1991, 2006) and Cordeiro (Cordeiro, 2005). Many patches are believed to have been isolated for 80 years (Newmark, 1991). Within this fragmented landscape are eight species of chameleon, three of which are considered forest-dependent (Tilbury, 2010; Measey *et al.*, 2013), including the IUCN endangered *Rhampholeon spinosus* (Matschie, 1892) and two species unassessed by IUCN: *Rhampholeon temporalis* (Matschie, 1892) and *Trioceros deremensis* (Matschie, 1892; Fig. 1). In addition to the East Usambaras, *R. spinosus* and *R. temporalis* also occur in the West Usambaras; *T. deremensis* also occurs in the Uluguru, Udzungwa and Nguru mountains. All surveys were between 846 and 1188 m elevation in the southern East Usambara Mountains in and around the Amani Nature Reserve (ANR; Fig. 2). This roughly corresponds to the elevational limitations of all three species – *R. spinosus*, > 700 m (Tilbury, 2010); *R. temporalis*, > 800 m (Emmett, 2004); and *T. deremensis*, > 800 m (Nečas, 1999).

Surveys

We used a distance-sampling approach to survey chameleons along 32.2 km of transects in the ANR and 11 smaller forest patches. Surveys were conducted at two time periods: (1) the cool dry season (September and October, 2010) – only in the ANR patch, totalling 16.8 km – and (2) the rainy season (February to April, 2011) – in all forest patches, totalling 15.4 km. For more details of transect placement, see Appendix S1 in Supporting Information. Surveys were conducted between the hours of 18:45 and 2:30 and > 24 h after transect placement to avoid disturbing chameleons away from the transect line. We used 120 lumen headlamps to locate chameleons at their roost sites. For each individual, we identified the species and measured its perpendicular distance from the transect line.

Vegetation sampling

To quantify habitat heterogeneity at a fine spatial scale, we selected 11 variables and sampled them in 5 × 5-m plots at 25-m intervals along each transect. In each plot, we visually estimated the proportion of vegetation cover at heights of (1) 0–0.5 m, (2) 0.5–2 m, (3) and 2–5 m, (4) measured canopy cover from the plot centre using a spherical densiometer (in each of four cardinal directions), (5) measured leaf litter depth using a ruler at four evenly-spaced locations, (6) counted the number of small (< 10 cm DBH) and (7) large (≥ 10 cm DBH) trees; and visually estimated the categorical cover (none, small, medium or large amount) of several plants that can dominate small areas of forest and alter vegetation structure including, (8) ferns, (9) vines, (10) *Dracaena* sp., and (11) the invasive tree, *Maesopsis eminii*. To reduce dimensionality of the vegetation data we conducted principal components analysis in the R package 'vegan' (Oksanen

Table 1 Characteristics of the 12 forest patches surveyed in the East Usambara Mountains of Tanzania as well as counts of the number of chameleons observed in each patch (for each species included in models). Isolation is measured as the distance to the nearest surveyed patch

Patch	Area (ha)	Isolation (m)	Transects (*n*)	Distance surveyed (m)	*Rhampholeon spinosus* (Matschie, 1892)	*Rhampholeon temporalis* (Matschie, 1892)	*Trioceros deremensis* (Matschie, 1892)
1	15.97	1742	10	1000	0	31	0
2	34.17	10	12	1200	1	44	3
3	16.72	127	10	1000	0	5	5
4	3.39	127	14	1165	0	0	0
5	3.94	270	9	933	1	6	2
6	12.92	562	10	1000	14	29	8
7	0.95	45	14	560	0	0	0
8	86.79	238	16	1600	1	42	8
9	84.78	238	14	1641	1	34	5
10	38.18	562	12	1200	0	8	3
11	721.9	10	90	19905	28	673	244
12	19.6	580	10	1000	0	10	0

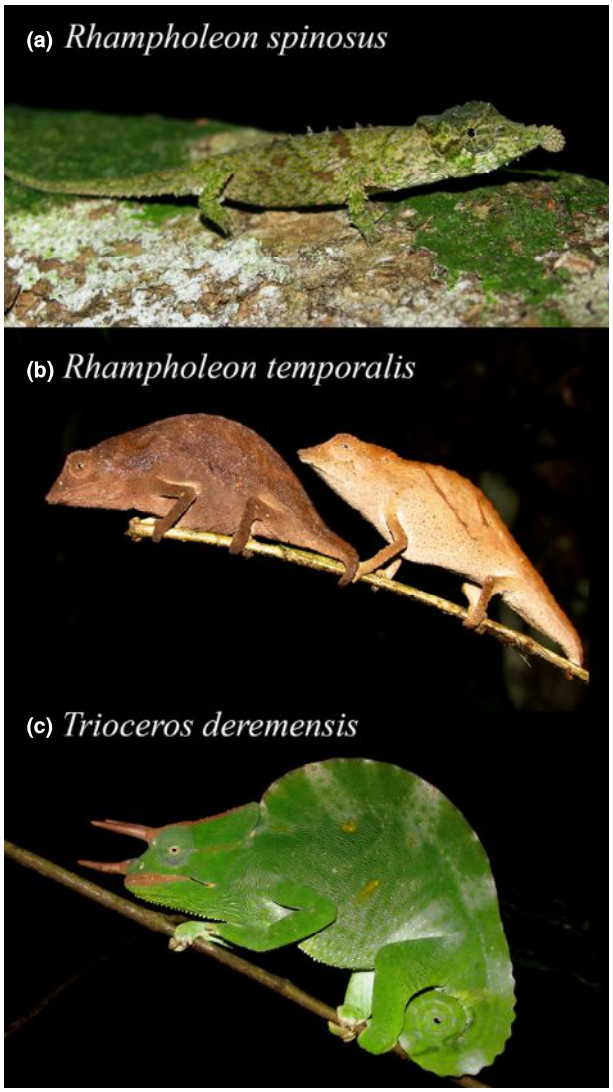


Figure 1 Our study species included (a) *Rhampholeon spinosus* (Matschie, 1892): a small (up to ~ 50–55 mm snout-vent length, 3–3.5 g), tree-dwelling chameleon; (b) *Rhampholeon temporalis* (Matschie, 1892): a small (up to ~ 55–60 mm snout-vent length, 4.5–5 g) leaf litter chameleon; and (c) *Trioceros deremensis* (Matschie, 1892): a large (up to ~ 150–160 mm snout-vent length, 60–80 g), tree-dwelling chameleon. All are forest-dependent species with limited geographical ranges.

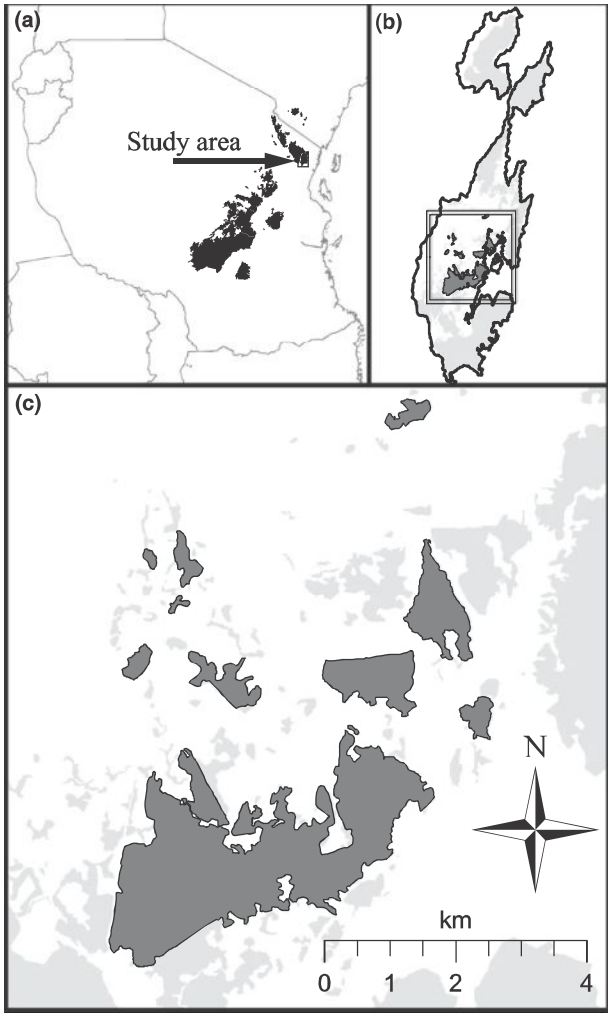


Figure 2 (a) Tanzania, with Eastern Arc Mountains in black and an arrow and small box depicting the location and extent of panel b. (b)The East Usambara Mountains, with forest cover (hand-traced from Google Earth® imagery) in light grey and a box depicting the extent of panel c. (c) The 12 forest patches included in this study are dark grey and were ground-truthed by walking the perimeter with a handheld GPS unit. The largest and southernmost surveyed forest patch is part of the Amani Nature Reserve.

et al., 2012). Although principal components analysis (PCA) does not require multivariate normal data, inference based on PCA is greatly strengthened when the data are multivariate normal, have linear relationships, and do not have multivariate outliers (Jolliffe, 2002). Therefore, before conducting PCA, we square-root transformed vegetation data to improve fit to multivariate normality, standardized the data, averaged it to the transect level, and ensured adequately linear relationships and a lack of strongly influential outliers. We used the first three axes, accounting for 53% of the original variation, for analysis (Table 2). PCA axis 1 generally reflected areas with little low-level vegetation cover and more upper-level vegetation cover. PCA axis 2 reflected more ground-level vegetation cover and less mid- to upper-level vegetation. PCA axis 3 represented areas with more large trees but a general decrease in medium-high vegetation.

Density estimation and modelling

Conventional distance sampling (Buckland *et al.*, 1993) focuses on estimating a detection function to quantify the decrease in frequency of observed individuals with horizontal distance from the centre of a sampling point or line transect. The result is an adjusted count of predicted 'true' abundance or, equivalently, density (e.g. abundance per sampling-unit area). Recent approaches allow for models that can formally estimate relationships between predicted densities and

Table 2 Coefficient values for the first three components of a principal components analysis of square-root-transformed and centered vegetation characteristics that were collected along all transects. For details on how each characteristic was measured, see section Vegetation Sampling. Vegetation characteristics with large loadings (> ± 0.3) are shown in bold to emphasize their contributions to an axis

	Component 1	Component 2	Component 3
% Variance	0.220	0.182	0.127
Vegetation cover: 0–0.5 m	**−0.339**	**0.342**	−0.222
Vegetation cover: 0.5–2 m	**−0.416**	−0.029	**−0.340**
Vegetation cover: 2–5 m	0.114	**−0.444**	**−0.303**
Leaf litter depth	**−0.310**	**−0.392**	0.101
Canopy cover	**0.340**	−0.252	0.238
Small trees	**0.345**	**−0.342**	**−0.314**
Large trees	0.133	0.043	**0.537**
Fern cover	0.147	**0.492**	0.000
Vine cover	−0.296	−0.291	0.230
Dracaena cover	−0.283	−0.073	**0.485**
Maesopsis cover	**0.401**	0.130	0.026

explanatory covariates that vary across sampling units (Hedley & Buckland, 2004; Royle *et al.*, 2004; Sillett *et al.*, 2012). The joint estimation of both detection and ecological processes is possible through a hierarchical modelling structure (Royle & Dorazio, 2008). Chelgren *et al.* (2011) generalized the model of Royle *et al.* (2004) for use with un-binned distance data collected on replicated line transects and estimated model parameters in a Bayesian framework to facilitate the incorporation of spatial and temporal random effects. A comprehensive description of the likelihood functions and joint posterior distribution of general models for both binned and un-binned distance data from line transects can be found in Eguchi & Gerrodette (2009).

We used a hierarchical Bayesian modelling framework to estimate chameleon densities with the line-transect distance data and examine relationships between densities and habitat attributes. Our model extends beyond previously published models to allow for the inclusion of covariates at both the local (transect) and landscape (forest patch) levels. While the data and parameter estimates were specific to each of the three chameleon species, the model structures remained consistent and, thus, are subsequently described without reference to species. Following Eguchi & Gerrodette (2009), the general objective of our approach was to compute the joint probability distribution, $P(N_i,\theta|y_i,n_i)$, where N_i is the unobserved true abundance at transect i, and θ represents the vector of model parameters describing the detection and ecological processes (*described below*). The observed data for each transect include y_i, the vector of observed distances to individuals, and n_i, the number of observed individuals; additional data included the covariates measured for each transect and forest patch.

For the detection process, we used a half-normal detection function in the likelihood of observed distances to individuals:

$$f(y|\sigma) = \frac{2}{\sigma\sqrt{2\pi}}\exp\left(-\frac{y^2}{2\sigma^2}\right) \quad (1)$$

where $y \geq 0$ and σ represents the standard deviation of the half-normal detection function. Given this specification (Eguchi & Gerrodette, 2009), the detection probability (P_i) for individuals at a transect can be calculated as follows:

$$P_i = \frac{\sqrt{2\pi\sigma^2}}{W}[\Phi(W/\sigma) - 0.5] \quad (2)$$

where W is the maximum observed distance to an individual and Φ represents the standard normal cumulative distribution function (subtracted by 0.5 to obtain the half-normal). Following standard procedures (Buckland *et al.*, 2001) we truncated the observed distances at the 95th percentile to remove outliers in the calculation of W. We did not truncate observations according to vertical height (*sensu* Jenkins *et al.*, 1999), as preliminary analyses using our hierarchical Bayesian distance-sampling model suggested no influence on the results. To account for unexplained variation in the form of the half-normal detection function and improve model fit, we allowed σ_i to vary by transect on the log scale:

$$\log(\sigma_i) = \mu_\sigma + \epsilon_{\sigma_i} \quad (3)$$

where μ_σ is the log-scale mean and ϵ_{σ_i} is normal random error. We specified the number of observed individuals as binomially distributed: $n_i \sim \text{Binomial}(N_i,P_i)$. Thus, the count of individuals at each transect was a function of the unobserved true abundance (N_i) and the detection probability (P_i) of all individuals located between the centreline (distance = 0) and W (distance = truncated maximum observed).

The ecological process models described the relationship between variation in abundance and habitat attributes at two scales, with random error to capture unexplained variation at each scale. The unobserved true abundance was a Poisson random variable, $N_i \sim \text{Poisson}(\lambda_i,A_i)$, where $\lambda_i = E[N_i]$ and $A_i = 2WL_i$, accounting for changes in the expected abundance according to the area sampled by a transect of length L_i. We specified a linear model of expected abundance on the log scale:

$$\log(\lambda_i) = \mu_f + \boldsymbol{X_i\beta} + \epsilon_{\lambda_i} \quad (4)$$

where μ_f is the log-scale mean abundance of forest patch f within which transect i is located; $\boldsymbol{X_i}$ is the vector of values for transect-level covariates (PCA axes 1–3, edge distance, season); $\boldsymbol{\beta}$ is the vector of regression coefficients for transect-level covariate relationships; and ϵ_{λ_i} is normal random error across transects. Transect-level covariates were not highly

correlated (Pearson's r ranged from 0.04 to 0.38). We also constructed a linear model for patch-level mean abundance (μ_f):

$$\mu_f = \mu_0 + Z_f\gamma + \epsilon_{\mu_f} \quad (5)$$

where μ_0 is the log-scale mean abundance across all patches; Z_f is the vector of values for patch-level covariates (patch area, between-patch distance); γ is the vector of regression coefficients for patch-level covariate relationships; and ϵ_{μ_f} is normal random error across patches. Patch-level covariates were also not highly correlated (Pearson's $r = -0.25$). We did not include interaction terms for any covariates as we did not hypothesize any significant interactions and because additional parameters would have decreased our model's power to detect other relationships. We assessed the importance of regression coefficients based on the estimated effect sizes and credible intervals; significant evidence for a covariate effect was indicated when the 95% credible interval (CRI) did not overlap zero, while strong evidence was indicated with a large effect size (median parameter estimate).

We estimated the joint posterior distributions of all model parameters using WinBUGS (Lunn *et al.*, 2000) via R with the R2WinBUGS package (Sturtz *et al.*, 2005). Our BUGS model code is presented in Appendix S2. Forest patch area and between-patch distance measures were log10 transformed and standardized to have a zero mean and unit variance. We used vague priors for model parameters, including diffuse normal distributions for regression coefficients and uniform distributions on the standard deviations for variance parameters (Appendix S2). The small sample size of *R. spinosus* observations necessitated a weakly informative prior for μ_σ (Appendix S2). Markov-chain Monte Carlo (MCMC) sampling for the model comprised three chains of 60,000 iterations after a burn-in of 15,000 iterations and a thinning rate of 15. Model convergence was assessed by examining trace plots of the posteriors and ensuring that the Gelman-Rubin statistic was < 1.1 for each parameter (Gelman *et al.*, 2013). Model goodness-of-fit was assessed with a posterior predictive check (Gelman *et al.*, 1996, 2013), similar to parametric bootstrapping, where the distribution of discrepancies between expected and model-generated values is compared to that between expected and actual values. We used a chi-squared discrepancy measure, $\Sigma_i\ (x_i - e_i)^2/e_i$, where x_i is either a generated or actual value for observation i and e_i is the expected value; this summation is calculated at each model iteration to produce posterior distributions for the summed discrepancies of generated and actual values. Good model fit is suggested when the proportion of posterior values above or below a 1:1 relationship is near even (0.50), while poor fit is indicated when the proportion is > 0.95 or < 0.05.

Estimating changes in total population size

To estimate current and historical population sizes, we used the methods of Ewers *et al.* (2010). First, we developed maps of forest cover for the East Usambara Mountains manually in Google Earth®, using imagery from 21 Jan 2003, 3 Jan 2003, 16 Dec 2002 to 8 May 2002. Similar to previous studies (e.g. Newmark, 1998; Burgess *et al.*, 2007; Hall *et al.*, 2009), we assumed that the East Usambara plateau was entirely forested historically. Therefore, our historical land cover most closely resembles the region prior to 2000 years ago, but is likely similar to the land cover in the area prior to the rapid extensive deforestation associated with the European colonial periods of the 20th century. Second, we calculated patch sizes using FRAGSTATS v4 (McGarigal *et al.*, 2012) and a raster of forest cover at 10-m resolution. Distance to the edge of the patch was calculated for each cell using the Euclidean distance tool in ArcGIS® 10 (Environmental Systems Research Institute (ESRI), 2011). Patch isolation had a weak relationship with population density, and thus, we excluded it to produce a more parsimonious model for the spatial projection procedure. Vegetation principal components were also excluded because a lack of fine-scale spatial data on vegetation characteristics for our study area (beyond areas we sampled) precluded their use as predictors of chameleon densities in unsampled areas. To avoid extrapolating beyond the data used to generate the model, we assigned historical forest cover the maximum sampled patch area and the maximum edge distance observed in the current landscape. Third, we used the hierarchical distance-sampling model above to relate land-cover characteristics to population density. We estimated densities for the rainy season (Feb.–April) because all forest patches were surveyed during this period and because we believe the rainy season estimates to be more representative of population densities (see discussion for details). Fourth, we extrapolated the model over the East Usambara plateau for areas > 850 m elevation (230 km^2 total), corresponding to the elevations where surveys were conducted. We incorporated uncertainty by using the full posterior distributions of the relevant model parameters, allowing us to calculate the precision of derived parameters (e.g. population size). Finally, we used this extrapolation to derive total current and historical population sizes and the change in population size between time periods. To draw inferences about species' entire ranges, we calculated Extents of Occurrence and Areas of Occurrence (International Union for the Conservation of Nature (IUCN), 2012b) using the estimates of Eastern Arc forest cover presented in Hall *et al.* (2009) along with species-specific elevational limitations.

RESULTS

Chameleon detections and densities

We observed 1262 chameleons, including 46 *R. spinosus*, 882 *R. temporalis* and 334 *T. deremensis*. The hierarchical models of density for each species exhibited adequate convergence and fit according to our model diagnostics. The proportions of summed chi-squared discrepancies for model-generated versus actual observations (where 0.5 suggests good model fit

and values near 0 or 1 suggest poor model fit) were 0.48, 0.42, 0.39 and for *R. spinosus*, *R. temporalis* and *T. deremensis*, respectively. Detection probabilities for individuals located within the sampling width of our transects were similar for each species: 0.67 (0.43–0.91 [95% CRI]) for *R. spinosus*, 0.57 (0.53–0.62) for *R. temporalis* and 0.56 (0.50–0.63) for *T. deremensis*. The average densities were highly variable across the species, ranging from a low of 0.8 ha^{-1} (0.2–2.9 ha^{-1}) for *R. spinosus* to a high of 32.4 ha^{-1} (21.2–49.1 ha^{-1}) for *R. temporalis*, with *T. deremensis* towards the lower end at 1.6 ha^{-1} (0.7–3.5 ha^{-1}). Within each patch, *R. temporalis* was by far the most abundant species (Fig. 3).

Patch-level covariates

Median coefficient estimates for the relationship between patch area and population density were positive for all three species, though estimates were not significant for *R. spinosus* and *T. deremensis* and indicated considerable uncertainty (Fig. 4). Median coefficient estimates for the relationship between patch isolation and population density were near zero for *R. spinosus* and *T. deremensis* and slightly positive for *R. temporalis*, but none were significant (Fig. 4).

Local-level covariates

The median coefficient estimates for the distance to the edge of the patch and the season in which the survey was conducted were relatively large compared to the vegetation covariates (Fig. 4), indicating strong effects on population density. All three species tended to have lower densities near edges; coefficients were significant for both *R. temporalis* and *T. deremensis*. While *T. deremensis* density was higher in the dry season, *R. spinosus* and *R. temporalis* densities were higher in the rainy season. The three vegetation PCA covariates had small coefficient values with low uncertainty for all three species; estimates for components 2 and 3 for *R. temporalis* and *T. deremensis* were significant (Fig. 4a,c), suggesting that their densities tend to increase with more ground-level vegetation cover (PCA 2) and large trees (PCA 3) and less mid-storey vegetation cover (PCA 2 and 3). For all model parameter estimates, see Tables S1–S3.

Population size estimates

Estimated population sizes varied considerably among species (Table 3), but all were strongly influenced by accounting for detection probabilities. Detection-adjusted population estimates were 49–79% higher than detection-naïve estimates (Table 3). All species have likely declined drastically (58–62%) from historical levels, but changes in population size are not evenly distributed across the landscape or limited to areas that have lost forest cover (Fig. 5). While the bulk of the changes in population sizes coincide with habitat losses,

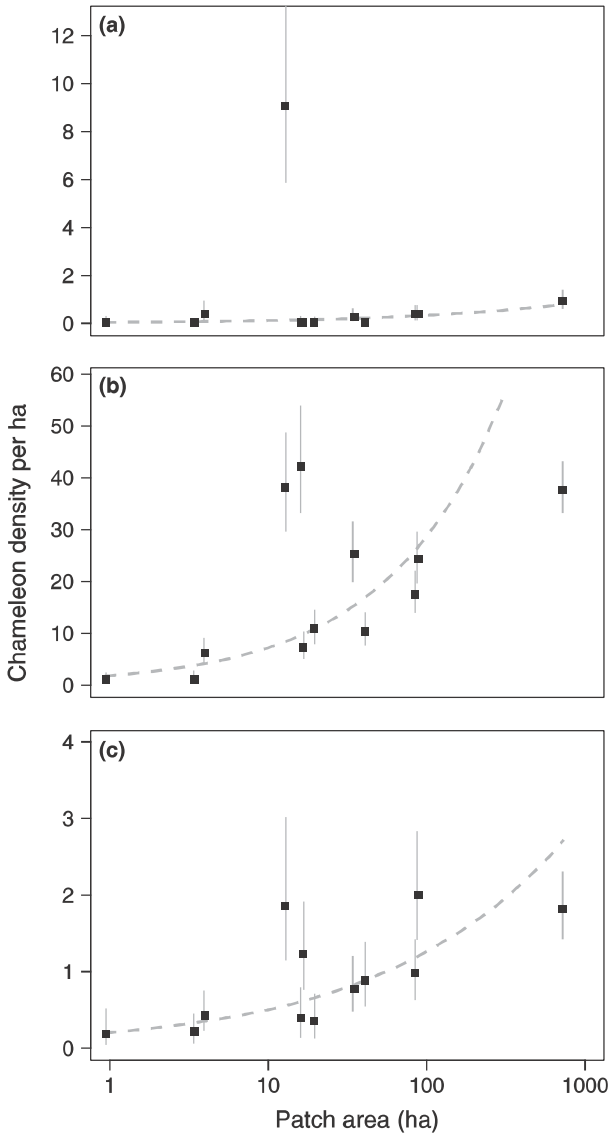


Figure 3 The predicted effect of patch area on (a) *Rhampholeon spinosus* (Matschie, 1892), (b) *Rhampholeon temporalis* (Matschie, 1892), and (c) *Trioceros deremensis* (Matschie, 1892) densities. Points with vertical lines represent median estimated densities with 95% credible intervals for each forest patch. Dashed lines are the model-predicted densities.

the configuration of the remaining habitat exacerbated estimated declines by an additional 30%. Our model predicts that the interiors of large forest patches have experienced the smallest declines in chameleon populations. Because many of these large forest patches are part of nature reserves, the majority of the remaining populations of all three species are located in protected forests (Table 3).

DISCUSSION

By accounting for changes in forest cover, species-specific detection, and processes at local and landscape scales that shape sensitivity to fragmentation, we were able to estimate

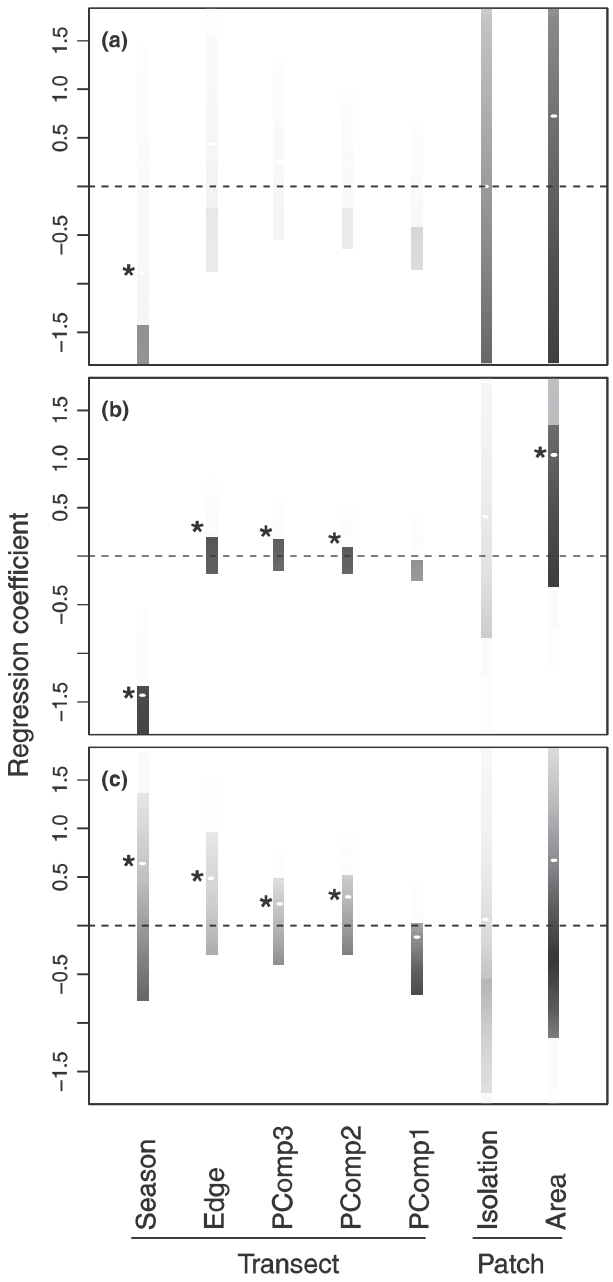


Figure 4 Regression coefficient values from a hierarchical Bayesian distance-sampling model of (a) *Rhampholeon spinosus* (Matschie, 1892), (b) *Rhampholeon temporalis* (Matschie, 1892) and (c) *Trioceros deremensis* (Matschie, 1892) densities. The distribution of posterior values for each regression coefficient is presented as a vertical line of varying darkness. Within the vertical distribution line, median values are indicated with a small, horizontal white line. Coefficients whose 95% credible interval did not overlap 0 have an asterisk above them. Species with a positive coefficient value for 'Edge' increase in density with increasing distance from the edge, while species with a positive coefficient value for 'Season' have higher density in the dry season (September–October) than the rainy season (February–April).

that forest-dependent chameleons in the East Usambara Mountains have likely declined by 60% from historical levels. Below, we discuss the influence of landscape characteristics at each spatial scale and also consider the range-wide habitat conditions for each species.

Local-level correlates of chameleon density

Overall, distance to the edge of a patch and the season in which we conducted surveys were better predictors of chameleons' densities than vegetation characteristics. Although our model supports a relationship between vegetation principal components and chameleon densities, the effects of vegetation were small. This is likely because our surveys were limited to forested areas where other factors more strongly influence chameleon densities. One of those factors appears to be the distance from the patch edge. Although studies of other chameleon species have observed higher chameleon densities along edges (e.g. Jenkins *et al.*, 2003; Andreone *et al.*, 2005; Metcalf *et al.*, 2005), our results suggest that our focal species are more common in the forest interior. Guidebook reports that our focal species prefer edges (e.g. Tilbury, 2010) are based on limited and often anecdotal information, rather than systematic, randomly-placed surveys such as ours. Chameleons near edges may also be negatively impacted by altered microclimatic conditions (Newmark, 2001; Ewers & Banks-Leite, 2013) or collection/hunting, which has been shown to act synergistically with fragmentation in other systems (Laurance & Cochrane, 2001; Peres, 2001; Thornton *et al.*, 2011). Further, limited previous surveys on chameleon in our study area suggest that chameleon richness is greater near forest edges (Patrick *et al.*, 2011), which may suggest greater interspecific competition near edges. Season also influences estimated chameleon densities. The seasonally-breeding *T. deremensis* populations are inflated by a birth pulse immediately prior to our dry season surveys, while the continuously-breeding *R. temporalis* appears to undergo partial-population aestivation during the dry season. Little is known about *R. spinosus* reproduction or aestivation, but given its similar size and close relation to *R. temporalis* (Matthee *et al.*, 2004), aestivation may also explain its seasonal variation in apparent density.

Patch-level correlates of chameleon density

Although other studies have suggested that edge effects create apparent area effects (Banks-Leite *et al.*, 2010), we accounted for edge effects in our model design and still observed area effects. Higher extinction probability in smaller patches (MacArthur & Wilson, 1967) may also cause area effects. We did not observe any of our three focal species in either of the two smallest patches sampled, despite the patches being relatively accessible (having short isolation distances). We do not believe the lack of sightings was the result of observation error because we did observe non-forest-dependent chameleon species in these patches and the two patches combined received more survey effort than nine of the other 10 individual patches, each of which had at least nine sightings of the three target species. Patch isolation was a poor predictor

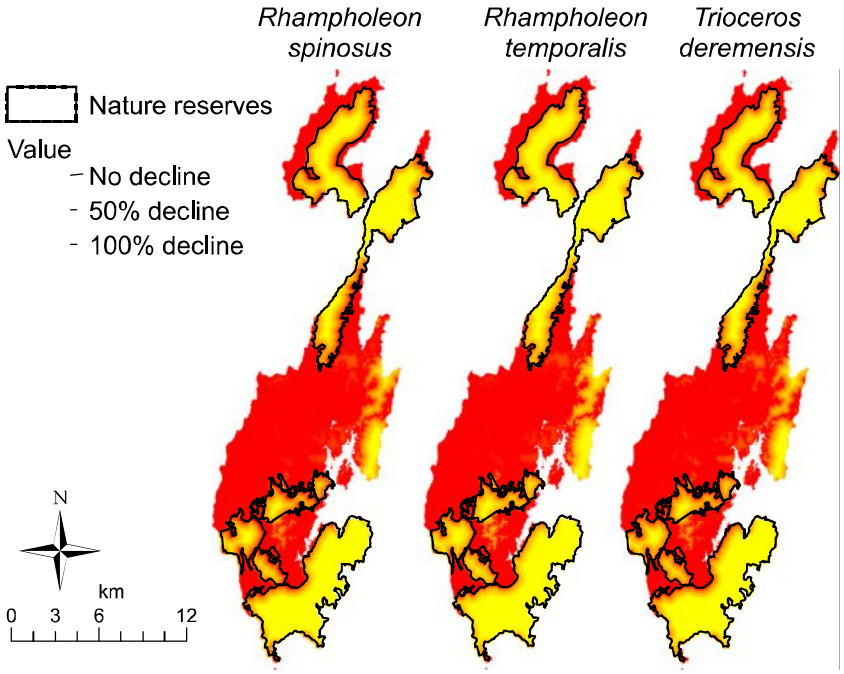


Figure 5 Projected change in abundance (estimated change in populations size (current minus historical) divided by the estimated historical population) of *Rhampholeon spinosus* (Matschie, 1892), *Rhampholeon temporalis* (Matschie, 1892) and *Trioceros deremensis* (Matschie, 1892) across the East Usambara Plateau above 850 m elevation. Dashed black lines delineate protected nature reserves. To estimate population sizes, we extrapolated each species' density across the study area using the entire posterior distributions of covariate values from a hierarchical Bayesian distance-sampling model. These maps were constructed using the coefficient values associated with the median population size estimate for each species. Forest patch area and the distance from the edge of a forest patch were included as covariates. Patch isolation was not included in the projection because of its poor predictive power, and vegetation variables were not included because they had small effect sizes and because they have not been mapped across the study area.

of chameleon densities, likely because isolation distances (10–1742 m, mean = 376 m) were beyond the dispersal threshold for low-motility chameleons to move through inhospitable matrix (tea plantation). In 1384 chameleon-days of radio-tracking and 73 nights of surveying, we never observed any chameleons in the matrix habitat. Even in forested habitat, large juveniles and adults of the largest and likely most mobile focal species, *T. deremensis*, maintain home ranges of ~ 2400 m^2 (minimum convex polygon) and move fewer than 100 m per day (unpublished data on 24 individuals radio-tracked for 15–242 days). Our ability to detect isolation effects may have been weakened further by our use of nearest-neighbour distance as an isolation metric (Tischendorf *et al.*, 2003; Calabrese & Fagan, 2004; Prugh, 2009).

Our results reveal larger but more variable effects of patch versus local characteristics on chameleon densities. Differences in the confidence associated with coefficient estimates for local and patch-level covariates are likely due to our sampling design. We surveyed 221 total transects (Table 1) and only 12 forest patches, giving the model more statistical power to estimate relationships with local-level covariates than with patch-level covariates. In addition to requiring a large number of replicates at each spatial scale of landscape variables, our modelling approach requires a large number of observations of each species (or enough species to treat species as a random effect). With only 46 observations for *R. spinosus*, we were unable to estimate density covariates with precision, although the median estimates of regression coefficients were similar to the more precise estimates that we obtained for *R. temporalis* (882 observations). Our inclusion of a random effect on the half-normal detection function parameter, σ_p, improved model fit, but at the cost of a slight loss in precision of abundance and regression coefficient estimates.

Landscape-level population declines

We estimate that *R. temporalis* declined 58% in the East Usambara Mountains, where 46% of forest area has been lost. This species has likely experienced even greater declines in the West Usambara Mountains (its only other known locality), where 73% of submontane forest has been lost between 1955 and 2000 (Hall *et al.*, 2009). Due to this forest loss and the fact that *R. temporalis* does not occur at low altitudes (Emmett, 2004), remaining suitable habitat for *R. temporalis* is just 15% of the total area of the mountains in which it occurs (~ 3078 km^2). Despite the relatively large estimated population size compared with the other species in this study, the concentration of *R. temporalis* into a few

Table 3 Population size estimates for chameleon species in forest habitat above 850 m elevation in the East Usambara Mountains. Each species has median estimates (with 95% credible interval) of the historical population size, a detection-naïve estimate of the current population size, our actual estimate current population size, the percentage change in population size, the population decline compared with the change in forest cover (a value of 100% would mean that the change in population size could be entirely accounted for by forest loss; values above 100% show additional impact of fragmentation), and the proportion of the median current population estimate that is found in protected nature reserves. Estimates of population sizes have greater uncertainty than estimates of the percentage change in population sizes because each estimate of the percentage change in population size comes from paired estimates of historical and current population sizes (each paired used the model parameter values from a single Markov-chain Monte Carlo iteration in our model fitting procedure)

	Historical population estimate	Detection-naïve current population estimate	Current population estimate	% Change	Decline as proportion of forest loss	Proportion in nature reserves (%)
Rhampholeon spinosus (Matschie 1892)	42,581 (56–25,927,480)	11,518 (52–5,991,198)	17,117 (78–8,903,549)	−60.3 (−69.1% to 97.2%)	−131.7% (−151.1% to 212.3%)	88.6
Rhampholeon temporalis (Matschie 1892)	3,771,458 (665,091–43,509,870)	900,045 (159,771–10,490,802)	1,569,116 (278,541–18,289,404)	−58.2 (−62.5% to −52.3%)	−127.2% (−136.6% to −114.4%)	87.8
Trioceros deremensis (Matschie 1892)	161,357 (12,195–3,349,245)	34,701 (2,953–686,517)	62,177 (5,292–1,230,097)	−62.1 (−67.9% to −52.1%)	−135.7% (−148.4% to −113.9%)	87.8

forest patches within its already limited range potentially leaves this species vulnerable to future habitat alteration and stochastic events.

Like *R. temporalis*, *R. spinosus* occurs only at high elevations in the East and West Usambara mountains (Tilbury, 2010), although it has been reported from slightly lower elevations (down to 700 m). Assuming similar habitat loss at these lower elevations, remaining suitable habitat for *R. spinosus* is ~ 16% of its extent of occurrence.

Trioceros deremensis is found in several Eastern Arc Mountains, and thus has the largest extent of occurrence of the three species (11,479 km^2). However, remaining forest cover in these mountains is just 22% of the total area (Hall *et al.*, 2009), substantially more forest loss than in our study area. Despite its limited population density in our study area, the range-wide population size of *T. deremensis* is likely much larger because it occurs in four distinct Eastern Arc Mountain blocks.

These population estimates have several conservation implications. First, we provide estimates of current population size and population decline for three rare, endemic chameleon species. As these are the first population estimates for these species, they will benefit Tanzanian wildlife managers and international conservation efforts. For example, the IUCN is currently assessing the vulnerability of two species (*R. temporalis* and *T. deremensis*) for the first time, and reassessing the endangered *R. spinosus*. When considering these species' overall vulnerability to habitat alteration, it is important to note that our estimates of population decline likely underestimate total declines across the species' ranges for several reasons: (1) deforestation has continued since our satellite imagery was taken (2002–2003), (2) we restricted our analysis to higher elevations (which have more protected areas than lower elevation forests in the East Usambaras), and (3) the East Usambaras have maintained more of their historical forest cover than any other Eastern Arc Mountain except the Ngurus (Hall *et al.*, 2009). Collectively, this suggests that these chameleon species have undergone large population declines, especially in the past ~ 130 years, when most habitat alteration has occurred (Conte, 2004; Hall *et al.*, 2009).

Second, our model identified spatial areas with the largest remaining chameleon populations. Over 87% of individuals in the study area occur in nature reserves. Relatively large chameleon populations also occur outside of nature reserves in the Eastern Central East Usambaras. This area is part of the Derema Corridor Catchment Forest Reserve, which is also protected, but receives less support to enforce protections than do nature reserves. Extraction of chameleons from intact forests does occur; all three study species are sold in the international pet trade, although the IUCN endangered *R. spinosus* has had an export quota of 0 since 2012 (Convention on International Trade in Endangered Species of Wild Fauna & Flora (CITES), 2013). Therefore, one potential method of protecting these forest-dependent species would be to incorporate more forest patches into existing nature

reserves. Finally, our spatially-explicit population estimates provide a baseline for future studies. Because of the large role that nature reserves are likely to play in the conservation of these species, comparisons may be particularly useful for assessing the efficacy of protected areas in chameleon conservation.

Conclusion

Our hierarchical, distance-sampling model allowed us to simultaneously incorporate uncertainty arising from estimation of the influence of covariates at different spatial scales, to propagate the uncertainty through all modelling steps, and to account for detectability. The results indicate that chameleon abundances in the East Usambara Mountains of Tanzania have declined drastically from predicted historical levels. Median estimates of decline are greater for all species than habitat loss alone would warrant. Remaining individuals in the study area are predominantly located in protected nature reserves; the amount of protection afforded by these reserves will likely determine the fate of these species in the East Usambaras.

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SUPPORTING INFORMATION

Additional Supporting Information may be found in the online version of this article:

Appendix S1 Details of transect placement.

Appendix S2 WinBUGS model code.

Table S1 Model parameter estimates (median, with 95% credible intervals) for *Rhampholeon spinosus* (Matschie, 1892).

Table S2 Model parameter estimates (median, with 95% credible intervals) for *Rhampholeon temporalis* (Matschie, 1892).

Table S3 Model parameter estimates (median, with 95% credible intervals) for *Trioceros deremensis* (Matschie, 1892).

BIOSKETCH

This research was conducted as part of **Philip L. Shirk's** Master's degree at Virginia Commonwealth University. He is currently a PhD student at the University of Florida examining the relationships between landscape characteristics and animals' abundances in an effort to inform conservation efforts.

Author contributions: P.L.S. conceived the ideas, obtained funding, collected data, conducted most analyses, and wrote the manuscript; D.W.L. developed the model specification and BUGS code, helped with model interpretation, and contributed to the manuscript; D.A.P. helped to obtain funding, helped conceptually, advised on fieldwork, and contributed to the manuscript; K.M.H. contributed valuable natural history information and logistical advice on conducting research in Tanzania; E.B.H. helped to obtain funding, helped conceptually, and contributed to the manuscript; J.R.V. advised P.L.S. and contributed extensively in all aspects of the project.

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