BIODIVERSITY RESEARCH

Applying resource selection functions at multiple scales to prioritize habitat use by the endangered Cross River gorilla

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ABSTRACT

Aim The critically endangered Cross River gorilla is a patchily distributed taxon for which habitat selection has been modelled only at coarse spatial scales, using remotely sensed landscape data and large-scale species distribution maps. These coarse-scale models fail to explain why Cross River gorillas (CRG) display a highly fragmented distribution within what appears to be a large, continuous area of suitable habitat. This study aimed to refine our understanding of CRG habitat use to inform conservation planning both for the subspecies and for other fragmented species of conservation concern.

Location Cross River gorillas occur only in a discontinuous distribution in the southern portion of the Cameroon-Nigeria border region, an area that represents one of Africa's biodiversity hotspots. This study was carried out in the Northern Mone-Mt. Oko region, part of the Mone/Mbulu forest system located in the Manyu division of the South-west Province of Cameroon.

Methods We used resource selection functions to understand habitat use by CRG at multiple scales. Specifically, we employed generalized additive models at the scale of the annual subpopulation range and conditional logistic regression at the scale of individual movements.

Results Cross River gorillas habitat selection is highly scale dependent. Localized measures of habitat quality strongly influenced selection at the subpopulation or landscape scale, while human activity and food availability were the best predictors of selection at finer scales.

Main conclusions Understanding why CRG do not occur in seemingly suitable habitat is crucial for designating critical habitat both within and between CRG subpopulations. Our results indicate that conservation planning to maintain critical habitat and connectivity among CRG populations will require an integrative, multi-scale planning approach incorporating large-scale landscape characteristics, human use patterns and CRG food availability.

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INTRODUCTION

In the face of habitat loss, degradation and fragmentation, understanding the characteristics that influence species occurrence and persistence is critical to preventing biodiversity loss (Kopp *et al.*, 1998). Rapid assessments of species' habitat requirements, including both ecological and anthropogenic factors, are necessary to inform land use and conservation decisions at multiple scales (Labonne *et al.*, 2003;

Dussault *et al.*, 2006; Desbiez *et al.*, 2009). Such assessments often rely on coarse-scale models due to the ease of access to remotely sensed habitat information such as land cover data. While coarse-scale inferences are useful for landscape-level conservation planning, they are also likely to miss micro- and meso-scale elements critical to species-habitat requirements, particularly for risk-sensitive and patchily distributed species (Howes & Lougheed, 2004; Sawyer *et al.*, 2011). In many instances, land cover data alone will be inadequate to

predict habitat constraints, and a combined approach that includes finer-scale analysis of factors influencing animal habitat selection is necessary for identification of habitat critical to the persistence of species of conservation concern (Hirzel & Le Lay, 2008; Mayor et al., 2009; Bjorneraas et al., 2011).

The Cross River gorilla (*Gorilla gorilla diehli*) is one such patchily distributed species for which habitat characterization is essential to effective conservation. One of the world's most endangered and least studied primates, the Cross River gorilla occurs only in a discontinuous distribution in the southern portion of the Cameroon-Nigeria border region (Bergl & Vigilant, 2007; De Vere et al., 2011; Bergl et al., 2012). Cross River gorillas (hereafter: CRG) are estimated to have as few as 300 individuals remaining, divided into 14 fragmented subpopulations within seemingly intact habitat (Sarmiento, 2003; Bergl et al., 2008, 2012; De Vere et al., 2011). To date, a lack of understanding of the relationship between CRG ecology and available habitat has hampered landscape conservation efforts. Available data has permitted only coarse-scale estimation of critical habitat for CRG persistence and connectivity based mainly on broad-scale, remotely sensed data (Groves, 2002; Bergl et al., 2012). These assessments indicate that the factors likely contributing to CRG habitat selection and suitability include: (1) habitat type, with preference for highland over lowland forest, and (2) human utilization, particularly hunting, with CRG preferring steeper, higher elevation areas that are farther from villages and harder for humans to access (Groves, 2002; McFarland, 2007; Bergl et al., 2012). Such macro-scale habitat selection models provide an important first step for predicting CRG distribution, but they must be refined by considering the determinants of suitability and connectivity at scales relevant to movement decisions by individuals (Doerr et al., 2011).

Resource Selection Functions (RSFs) represent an important tool to understand species-habitat requirements at multiple scales and provide theoretical foundations for applied habitat management decisions (Kopp et al., 1998; Howes & Lougheed, 2004; Hirzel et al., 2006). An RSF is a statistical model that indicates the probability of use of a particular resource/habitat type by a given individual or group and is used to identify non-random species-habitat associations and essential resources (Boyce & McDonald, 1999; Labonne et al., 2003; Boyce, 2006; Kirk & Zielinski, 2009). RSFs may be particularly valuable in conservation decision-making for patchily distributed species and can complement more macro-scale species distribution models by identifying critical habitat both within and between fragmented populations (Harris et al., 2008).

The influence of particular landscape characteristics on species' habitat use and movement within and between subpopulation patches will vary with scale, and both resource selection decisions and conservation/management actions are thus highly scale dependent (Gustine et al., 2006). RSF models can be applied at multiple scales in a hierarchical approach to understand the influence of scale and link macro-scale distribution models to decision-making by individual animals (Mayor et al., 2009). Because RSF models can consider habitat selection by individuals, groups, populations and taxa, they provide an important tool to incorporate scale into both ecological understanding and conservation decision-making, particularly for fragmented, risk-averse species (Meyer & Thuiller, 2006).

Johnson (1980) describes four orders of resource selection by species from coarse to finer spatial scales: (1) choice of the geographic range by a taxon; (2) choice of a use area (e.g. home or subpopulation range) within the geographic range; (3) use of a habitat component or area (e.g. forest patch) within the home range; and (4) selection of a specific resource (e.g. nest site, food source) within a selected area (Johnson, 1980; Buskirk & Millspaugh, 2006). Rarely do studies incorporate and communicate across multiple scales. To date, only the first order of selection has been examined for the CRG, due mainly to a lack of data at finer scales (Bergl et al., 2012). We used a multi-scale approach to assess resource selection at progressively finer scales by one CRG subpopulation living in the Mone Forest Reserve in Cameroon. Our three levels of analysis include: (1) coarse-scale selection of subpopulation range compared with available resources in the study area; (2) intermediate-scale selection of resources compared with available resources within the current subpopulation range; and (3) fine-scale selection of resources by a gorilla group compared with resources available within an average day's journey length of selected locales (McLoughlin et al., 2004; Perkins & Conner, 2004; Boyce, 2006; Ciarniello et al., 2007). By integrating resource selection across spatial scales, this study helps to define critical CRG habitat for both persistence within and connectivity among CRG subpopulations. It also endeavours to illustrate the utility of applying a hierarchical habitat selection framework to inform decision-making in conservation.

METHODS

Study site and data collection

Surveys to assess CRG habitat use were conducted in the Northern Mone/Mount Oko region. This region is part of the Mone/Mbulu forest system located in the Manyu division of the Southwest Province of Cameroon and represents one of Africa's biodiversity hotspots (Nku, 2004; Asaha & Fru, 2005; Forboseh et al., 2007; Fig. 1). The Northern Mone/Mount Oko region includes the northern portion of the 560 km^2 Mone River Forest Reserve, designated as a production forest by the national government, and the Southern portion of the Mbulu forest, called Mt. Oko (Fig. 1a). For more details about the study site, please see Appendix S1 in Supporting Information. The Mone/Mount Oko region contains at least one of the fourteen known subpopulations of CRG. Very little data on potential CRG locations within the region were available prior to this study, and little was known about if and how CRG utilize
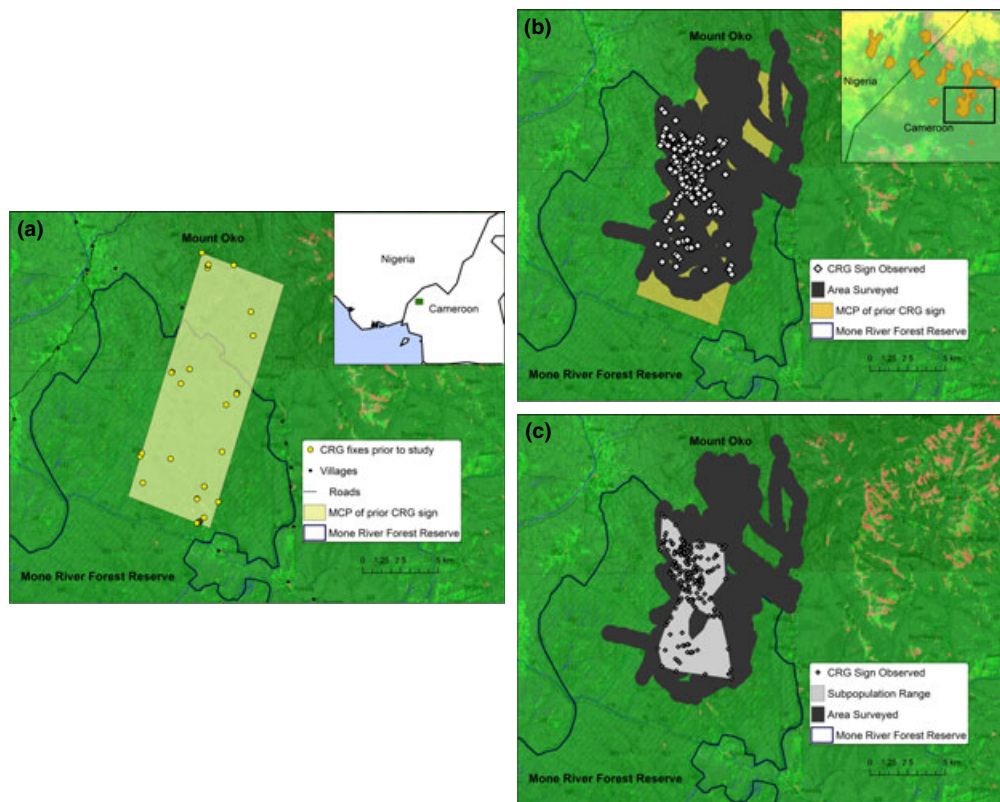
Figure 1 (a) Location of Cross River gorillas (CRG) sign observations prior to study period, collected by the Wildlife Conservation Society Takamanda Mone Landscape Project (*N* = 38). Minimum convex polygon created from prior observations to target study surveys. (b) Area surveyed during this study and all locations of gorilla sign observed. Inset of approximate CRG distribution, courtesy of Wildlife Conservation Society Takamanda Mone Landscape Project. (c) Area surveyed, CRG sign detected and resulting Mone CRG subpopulation range estimation (see Sawyer, 2012).

this portion of the landscape. Because the potential CRG habitat in the area is quite large, we calculated a minimum convex polygon (MCP) of gorilla sign locations (*N* = 38) over the previous 10 years in the Mone-Mt. Oko region (ESRI, 2011) to help facilitate targeted surveys (Fig. 1a). These location data were collected and generously shared by the Wildlife Conservation Society's Takamanda Mone Landscape Project. Please see Appendix S1 for more details. From November 2009 through August 2010, we conducted guided reconnaissance and travel surveys in and adjacent to the MCP to search for gorilla sign, and to measure CRG vegetative food species availability and habitat characteristics in sampling plots at 500 m intervals (McNeilage *et al.*, 2006; Kuhl *et al.*, 2008; Sawyer, 2012; Fig. 1b). Guided reconnaissance surveys follow the path of least resistance while deviating no more than 40° from a set compass bearing (Kuhl *et al.*, 2008) and were placed no more than 500–700 m apart to minimize the chance that gorilla use of any area went undetected (McNeilage *et al.*, 2006). When we found recent gorilla sign, we abandoned the compass bearing and followed the CRG feeding path (i.e. travel survey). A total of 262 km of surveys were walked in this manner (Fig. 1b). No CRG sign was observed in the Mt. Oko area during this study (Fig. 1b).

This study relied on indirect sampling methods (Doran *et al.*, 2002; Rogers *et al.*, 2004; Sunderland-Groves *et al.*, 2009). Specifically, we recorded CRG nest sites, trampled vegetation, dung and feeding sign (chewed, broken and discarded vegetation) and estimated the approximate date of use by the CRG for each sign. Please see Appendix S1 for detailed description of indirect data sampling. Nest sites and foraging signs remain intact and easily identifiable for many months (170–189 days; Williamson & Usongo, 1996; Brugiere & Sakom, 2001) and visible for even longer, and can be aged to reflect approximate (± 1 month) date of gorilla habitat use within the past year (Brugiere & Sakom, 2001; McFarland, 2007; Sawyer, 2012). Because confusion can occur between chimpanzee and gorilla nests in this landscape, trackers tried to use secondary indicators such as footprints, dung, feeding sign or vocalizations to ensure nest sites were correctly attributed to CRG. However, some signs may have been miss-attributed to CRG or chimpanzee. We thus repeated our analyses, described in the 'data analysis' section below, both (1) including chimpanzee sign and (2) excluding older gorilla sign, to examine how this potential misidentification would impact our conclusions. We address the implications of these potential errors in our discussion.

In addition to recording gorilla sign, we carried out visual habitat assessments within 477 ten-metre-diameter circular vegetation plots, placed at 500-m intervals along both guided and travel reconnaissance trails. Within sampling plots, we recorded the following habitat characteristics: habitat type, canopy cover, undergrowth thickness, dominant undergrowth type, slope, presence or absence of signs of human use and presence or absence of signs of gorilla use. Human sign recorded included: cartridges, traps, machete marks, trail demarcation, foot prints, huts/sheds and any other clear sign of forest product use. We also enumerated stem counts of vegetative (herbaceous/fibrous) CRG food species and presence/absence of seven important non-timber forest products (NTFPs) within sampling plots (S. Sawyer, unpublished data; Table 1). Important fibrous (vegetative) species were defined as those consumed on > 5% of the observed feeding trail days (Doran *et al.*, 2002; Ganas *et al.*, 2004; S. Sawyer, unpublished data). Logistical constraints prevented us from including fruit species, an important part of the CRG diet, in the analysis. Additional research will be necessary to monitor fruit species in the landscape and will provide essential information to improve upon out analyses. We recorded location coordinates for all CRG signs, sampling plots, human signs and other wildlife signs using a Garmin GPS and Cybertracker.

Data analysis

We developed resource selection models for three levels of spatial analysis using the survey data collected over the 10-month study period, which represented *c.* 20 months of gorilla use (McLoughlin *et al.*, 2004; Perkins & Conner, 2004; Buskirk & Millspaugh, 2006; Sawyer, 2012). To do this, we started by estimating the CRG subpopulation range using the Local Convex Hull modelling technique (Calenge, 2006; Getz *et al.*, 2007; Sawyer, 2012; Fig 1c). Please see Appendix S1 and Sawyer, 2012 for details of subpopulation range calculation.

We assessed resource selection by CRG at the scale of the subpopulation range by comparing habitat characteristics within the CRG subpopulation range to those available within the study area (McLoughlin *et al.*, 2004; Dussault *et al.*, 2006; Ciarniello *et al.*, 2007). Our second level of analysis compared habitat characteristics of areas where we found sign of gorilla use to overall availability of those habitat features within the current subpopulation range (Johnson, 1980). Our third level of analysis examined day-to-day habitat selection by individuals. Specifically, we paired used and neighbouring unused locations on a local scale to evaluate fine-scale patterns of habitat selection (Buskirk & Millspaugh, 2006; Godbout & Ouellet, 2010). For this third level of analysis, each location where gorilla use was confirmed was paired with five randomly selected available locations within a buffer distance deemed to be the average distance a gorilla

Table 1 Variables included in resource selection models for Cross River gorillas (CRG)

Variable	Description
CRG sign*	Presence or absence of signs of CRG use within approximately the last 10 months
Altitude	Elevation of plot (GPS measurement)
Search effort	Density of GPS tracklog points within a 1-km radius – indicator of time spent within 1 km of plot, generally longer on travel than reconnaissance surveys due to indirectness of CRG routes
Distance to village	Distance in kilometres to the nearest village
Distance to human sign	Distance to the nearest sampling plot where human sign was recorded
Slope	Categorical measure of steepness of slope, on a scale of 0–3
Habitat type	Categorical measure of habitat type: Montane forest, Ridge forest, Lowland forest, disturbed/secondary forest, bare soil
Canopy closure	Categorical measure of per cent canopy cover at centre of vegetation plot, scaled from 1 to 4
Understory thickness	Categorical measure of undergrowth density throughout plot, scaled from 1 to 4
Understory type	Dominant understory vegetation type: Herbs, Bushes, Lianas, Shrubs, Rocky/Open, Grass
Human sign (hunting proxy)	Measure of human impact, from 0 to 4 where 0: no human sign, 1: human sign visible from but not within plot, 2: plot on human path or including harvest sign, 3: past farming, clearing or burning evident, 4: current farm or village land. Human signs included: cartridges, traps, cutting sign, trail demarcation, foot prints, hut/shed, use of forest products (e.g. honey extraction). Most human sign was hunting related
Individual food species	Stem counts of common food species: *Cercestis camerunensis*, *Stylochaeton zenkeri*, *Palisota spp*, *Aframomum spp* and four additional herbaceous spp were tested
Total NTFPs (other human use proxy)	Number of seven of the main Non-Timber Forest Products present in the plot. NTFPs identified as present or absent included: Palm spp, Cola spp, Spices, Cattle Stick, Bush Mango, Country Onion, Bush Pepper and Fish Poison
Remotely sensed habitat type	Habitat type classified using Landsat Imagery: Primary Forest, Secondary Forest/Agriculture, Water, Rock/Bare Soil

NTFPs, non-timber forest products.
*Dependent variable.

can travel within a day (Cooper & Millspaugh, 1999; Compton *et al.*, 2002; Boyce, 2006; Buskirk & Millspaugh, 2006; Ciarniello *et al.*, 2007). This distance was conservatively set at 1.5 km based on observed daily travel distances of the ecologically similar eastern lowland gorilla (unpublished data; Yamagiwa *et al.*, 1994).

For the first two levels of analysis, we developed a generalized additive model (GAM) to create the resource selection function. This approach creates a probability of gorilla resource use in relation to habitat, food and human use variables using a logit link function with the gamlss command in R statistical package (Panigada *et al.*, 2008; R Development Core Team, 2010). Modelled variables are listed in Table 1. GAMs were fit using a reverse stepwise procedure with the stepGAIC function in R statistical package for a set of candidate variables including all habitat and human use measures, and the most frequently observed vegetative food species in the CRG diet (Carroll *et al.*, 1999; Kirk & Zielinski, 2009; S. Sawyer, unpublished data). The third level of resource selection analysis employed a conditional logistic regression approach, using the logit command in the survival package in R to compare CRG used sites with available resources in a 1.5-km buffer zone (Compton *et al.*, 2002; Duchesne *et al.*, 2010; Cockle *et al.*, 2011; Therneau, 2012).

For all three spatial scales, we tested for collinearity of candidate variables using variance/covariance matrices, and variables with a correlation coefficient (r) > 0.7 were not included together in the models (Ciarniello *et al.*, 2007; R Development Core Team, 2010). Where collinearity occurred, we retained the most easily measured habitat variable (e.g. elevation/slope rather than food stem densities). For predictor variables exhibiting correlation coefficient values between 0.6 and 0.7, we retained only the residuals of a linear regression of the more complex against the simpler habitat measure to identify any remaining unexplained effect. We used AIC values to select relevant variables (Burnham & Anderson, 1998; Zielinski *et al.*, 2004; Harris *et al.*, 2008; Horne *et al.*, 2008; Kirk & Zielinski, 2009), and we considered models comparable if the delta AIC was < 2.0 (Ciarniello *et al.*, 2007). For models with similar AIC values, we chose the model with fewer terms (Quinn & Keough, 2002). To minimize the effect of spatial autocorrelation, we included UTM coordinates as covariates in the model (Boyce & McDonald, 1999; Carroll *et al.*, 1999; Boyce, 2006). Additionally, we included GPS point density as a measure of search effort because travel reconnaissance surveys can lead to high concentration of search effort in areas where gorilla sign is found (Panigada *et al.*, 2008; Table 1).

RESULTS

Annual subpopulation range selection

Resource selection by CRG exhibited strong, nonlinear relationships with elevation, slope and distance to nearest village at all scales of analysis (Figs 2 & 3). At the coarsest scale of

analysis, variables retained in the final model predicting selection of the current CRG subpopulation range were generally localized measures of habitat quality (Table 2). Although habitat type did not have predictive power at the scale of subpopulation range selection, more localized habitat quality characteristics were significant. CRG showed preference for areas with more open canopy and understory, characteristic of light gaps, which may promote herb growth (White *et al.*, 1995). In addition, slope was important, and CRG selected their range within areas of 10–25% slope, indicating avoidance of both flat and very steep areas (Fig. 2, Table 2). Altitude was also significant, but contrary to findings of previous studies (Groves, 2002; Oates *et al.*, 2003; Bergl *et al.*, 2012), our best model suggested CRG selected mid-elevation areas over both low and high elevations
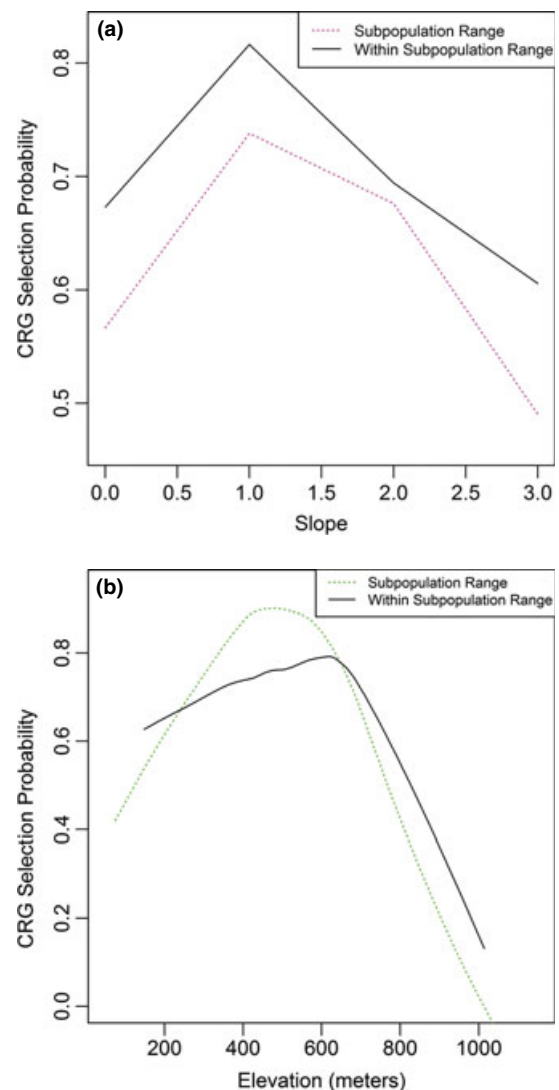

Figure 2 Habitat selection probabilities for Cross River gorillas in response to available (a) slope and (b) elevation reveal similar nonlinear patterns at both the subpopulation range (i.e. landscape) scale and at a finer within-range scale.
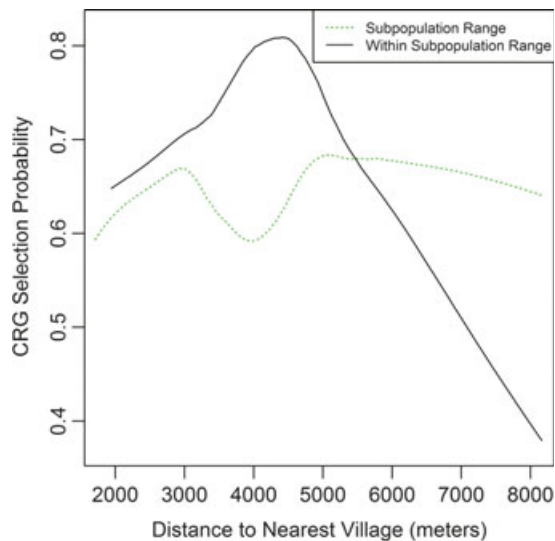
Figure 3 Probability of habitat selection by Cross River gorillas in relation to distances from the nearest village. Distance to nearest village was not a significant predictor of selection at the subpopulation range/landscape scale, but habitat selection within range showed significant selection of sites at intermediate distances from villages.

(Fig. 2, Table 2). While the study site averaged 740 masl (range 56–1744 masl), the average gorilla sign was observed at 504 masl (range 75–1207 masl). Additionally, 77% of gorilla signs observed were found below 650 masl. This likely represents an underestimation of lowland use, as we were often unable to attain GPS elevation readings at lowland sites. Finally, most measures of human use (i.e. human sign, distance to human sign) were not retained in the best model,

and distance to the nearest village was retained but was not significant (Fig. 3, Table 2), indicating a low importance of human resource use in subpopulation range selection. When chimpanzee sign were included, results varied only slightly. Both density of the important food species *Cercestis camerunensis* and presence of shrubs in the understory became additional significant predictors of CRG range. No variables dropped out of the best model.

Habitat use within the subpopulation range

Within the current CRG subpopulation range, food availability and human utilization were significant predictors of habitat selection, in addition to localized habitat quality indicators (Table 2). Similar to our macro-scale analysis, canopy openness and elevation were significant predictors of CRG habitat selection within the subpopulation range, but undergrowth thickness and slope were not significant at this finer scale. In addition, the two most commonly consumed herbaceous food species remained in the best model, with CRG selecting habitat with higher stem densities of these foods (unpublished data; Table 2, Fig. 4a). Measures of human use were negatively correlated with CRG habitat use within the subpopulation range, indicating avoidance by CRG of heavily exploited areas (Table 2, Fig. 4b). The majority of human sign encountered (873 of 893 signs) was either directly related to hunting (i.e. cartridges, snares; $n = 404$) or indirectly related (i.e. hunting trails and huts; $n = 469$). Thus, human sign in this study should be considered a proxy for hunting pressure, while NTFP presence should provide a proxy for other harvesting. However, even accounting for search effort, areas nearer to villages were slightly preferred to farther ones within the range (Fig. 3). Finally, presence of forest products (NTFPs) impor-

Table 2 Predictor variables retained in the best resource selection functions for Cross River gorillas at three spatial scales of selection

Selection scale	Subpopulation range		Within subpopulation range		Within day journey distance	
Covariate*	Coefficient	P	Coefficient	P	Coefficient	P
Habitat type	–	–	–	–	–	–
Altitude	**−0.002**	0.000	**−0.003**	0.020	**−0.004**	0.000
Slope	**0.342**	0.042	–	–	–	–
Canopy closure	**−1.554**	0.000	**−1.892**	0.000	**−1.860**	0.000
Undergrowth thickness	**−0.423**	0.010	–	–	0.272	0.059
Liana understory	–	–	–	–	**−0.808**	0.002
Distance to village	−0.0003	0.079	−0.0002	0.497	–	–
Human sign	–	–	**−0.866**	0.000	**−1.104**	0.000
Distance to human sign	–	–	**0.006**	0.043	**0.003**	0.025
Total NTFPs present	–	–	**−0.414**	0.001	**−0.225**	0.004
Cercestis camerunensis	–	–	**0.053**	0.014	**0.025**	0.044
Stylochaeton zenkeri	–	–	0.014	0.052	**0.018**	0.000
Aframomum spp	–	–	–	–	0.070	0.051
Palisota spp	–	–	–	–	0.034	0.065

NTFPs, non-timber forest products.

*Spatial coordinates and search effort retained in all models.

Values in bold are statistically significant predictors of CRG selection ($P \leq 0.05$).
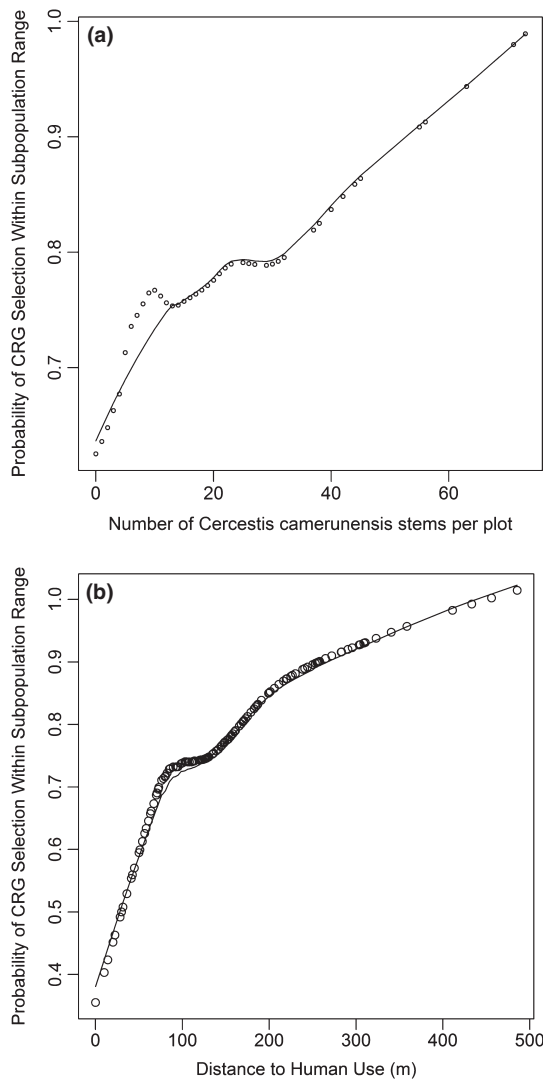
Figure 4 Probability of habitat selection within the Cross River gorilla subpopulation range in relation to (a) availability of the most preferred food species and (b) distance to human activities.

tant for human use was also negatively correlated with gorilla habitat selection, although no relationship was detected between the distribution of forest products and preferred CRG food species (Table 2). When chimpanzee signs were included in the analysis, while human sign no longer remained in the best model, distance to human sign did. The food species *C. camerunensis* dropped out of the best model, likely because it became significant at the subpopulation range scale instead. When older gorilla sign was excluded, human disturbance remained significant, but distance to nearest human sign did not. Elevation dropped out of the model, while slope remained instead.

Habitat use within daily travel distance

At the finest scale of habitat selection – within an average day journey length from CRG sign – availability of moni-

tored staple food species was a primary predictor of CRG habitat selection. The availability of the four most commonly eaten herbaceous species, *C. camerunensis*, *Stylochaeton zenkeri*, *Aframomum* sp and *Palisota* sp, was positively correlated with CRG habitat selection (Table 2). As in the coarser models, measures of human impact (both hunting and other harvest activities) were significant at the finest scale, with human use and proximity to human use negatively affecting CRG habitat selection (Table 2). Measures of local habitat quality were also significant predictors of CRG selection, with selection towards more open, mid-elevation areas, and against those areas dominated by liana understory and with high availability of NTFPs (Table 2). When older gorilla sign was excluded *Aframomum* sp dropped out of the model, but *Palisota* sp became more significant. Proximity to human use dropped out of the model, but presence of human use became more significant.

DISCUSSION

This study developed RSFs to identify factors critical to the distribution of the Cross River gorilla at multiple spatial scales. In so doing, it begins to shed more light on the forces driving the current distribution of CRG and confirms that resource selection by CRG, like that of many wide-ranging species, is highly scale specific (McLoughlin *et al.*, 2004; Boyce, 2006; Dussault *et al.*, 2006; Baasch *et al.*, 2010). While our data collection was limited by many factors, and our results should be interpreted with caution, we hope this study will both help inform conservation measures and also encourage further research to flesh out our findings.

To date, the factors limiting the fragmented distribution of CRG have not been well understood, as coarse-scale models indicate high levels of suitable but unoccupied forest in the region (Oates *et al.*, 2003; Bergl *et al.*, 2008, 2012). While underlying causes for extirpation of CRG from previously inhabited sites remain largely unknown, hunting may have been a major contributor to general population declines (Bergl *et al.*, 2008, 2012; Thalmann *et al.*, 2011). This study indicates that while remotely sensed habitat characteristics like slope and elevation may be useful predictors of CRG distribution at the coarse scale, human activities and food availability become more important to finer-scale selection, where CRG likely make day-to-day movement decisions. These findings highlight the utility of hierarchical RSFs to better understand resource use by focal species. However, we were only able to include areas occupied by, and directly surrounding, one of the 14 subpopulations. Thus, results should be interpreted conservatively and, as similar data become available for additional subpopulations, more robust conclusions will evolve.

Subpopulation range selection by CRG preferentially included areas with partially open canopy and undergrowth cover. This may indicate a preference for highly herbaceous areas (White *et al.*, 1995), as herbaceous vegetation is a keystone resource for gorillas and can serve as an important
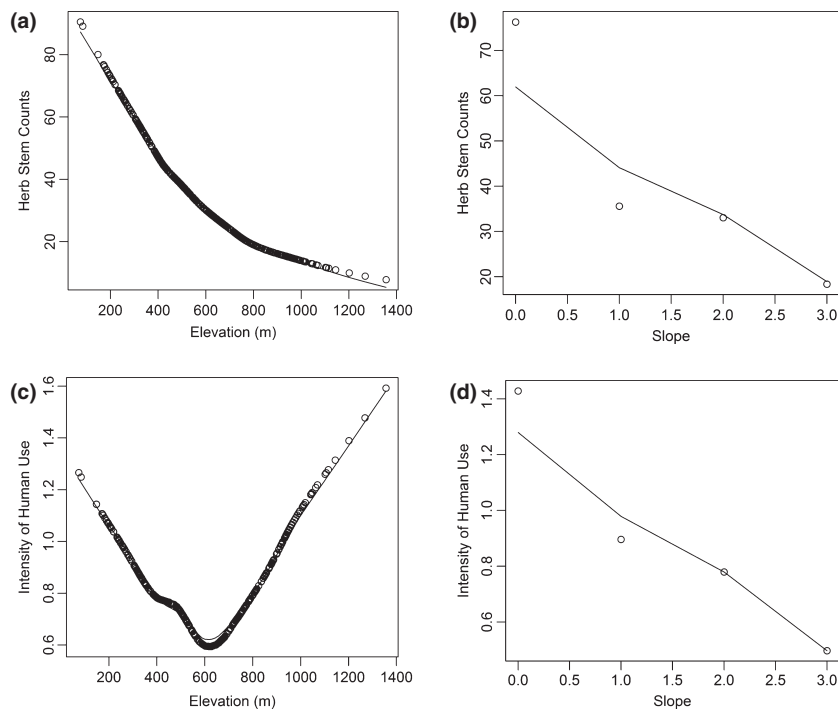
Figure 5 Availability of herbaceous plants preferred by Cross River gorillas was negatively correlated with both (a) elevation and (b) slope. Intensity of human activities had a significant and nonlinear relationship with elevation (c) and was negatively correlated with slope (d).

buffer during periods of low fruit availability (Yamagiwa *et al.*, 1994, 2005; Brugiere & Sakom, 2001). Selection at the subpopulation range scale also showed preference for areas at mid-elevation levels with low to mid-slope. These results represent a divergence from more coarse-scale studies, which highlight steep slope, highland forest areas as highly suitable for the CRG (Groves, 2002; Sunderland-Groves, 2008; Bergl *et al.*, 2012). An explanation for the observed differences of this study to previous findings may be the failure of macro-scale analyses to incorporate trade-offs between resource abundance and potential risks (Fig. 4). Resource selection often requires trade-offs between food availability and exposure to potentially detrimental factors (Dussault *et al.*, 2006; Bastille-Rousseau *et al.*, 2010), and food availability in this system is poorly predicted by coarse-scale habitat type. Our observation of selection by CRG of mid-elevation and inter-mediate slopes at the subpopulation range scale may thus represent a compromise between attraction to staple food species (more abundant at lower elevations) and avoidance of human activity, particularly hunting (also higher at lower elevations) (Fig. 5). To date, food distribution has often been overshadowed by hunting impacts in understanding of CRG ranging patterns. This study highlights the importance of both factors, and their potential interaction, in determining current CRG distribution. We were unable include fruit food species in our analysis, which will undoubtedly exert significant forces on CRG ranging. Future studies should incorporate phenology and dietary analysis to better understand fruit in the CRG diet, as well as its spatial and temporal distributions in the landscape.

Although human activity seemed to have little influence on CRG habitat use at the scale of subpopulation range selection, likely an indication that human use is fairly ubiquitous at the largest scales within the landscape, new patterns of resource selection emerge within this range. CRG select areas of lower human use within their subpopulation range and at the scale of daily journey distances (Fig. 4b). While human activities in the region include collection of NTFPs, hunting activities appear to be the strongest determinate of CRG habitat use. Like many wildlife species, CRG are threatened by hunting, which operates both directly on species' abundance by removing individuals, and possibly indirectly by raising stress levels, changing behaviour and reducing reproductive output (Robinson & Bodmer, 1999; Wilkie & Carpenter, 1999; Pauli & Buskirk, 2007; Bergl *et al.*, 2012). Wildlife harvest studies in the region indicate that one to three CRG are harvested annually, although this is likely an underestimate (Oates *et al.*, 2003; Sawyer & Sawyer, 2011). Additionally, although most local hunting does not target gorillas, hunting of other species is common in the area (Mboh & Warren, 2007), which may indirectly affect CRG through stress and behavioural responses, resulting in avoidance of areas associated with human utilization and leading to decreased connectivity among subpopulations.

In addition to human impacts, availability of staple food species influenced CRG habitat selection within the subpopulation range. The two most common herbaceous/vegetative species in CRG diet were shown to influence habitat use on a broader scale, while at a finer scale, where individual movement decisions are made, all four of the staple herba-

ceous food species influenced habitat use (S. Sawyer, unpublished data). Food is an important limiting factor to species' abundance and distribution, and many primate populations have been observed to decline significantly when key food species are selectively removed through logging or other processes (Chapman *et al.*, 2006). Studies examining gorilla distributions indicate that western gorillas occur at higher densities in areas where their staple foods are most abundant (Rogers *et al.*, 2004), and that food availability has important implications for population dynamics, including carrying capacity (Nkurunungi *et al.*, 2004), sociality and ranging patterns (Doran-Sheehy *et al.*, 2004). Food availability has largely been ignored in landscape-scale connectivity and conservation modelling for CRG due to a lack of data. However, this study indicates that coarse-filter habitat type may have little correlation with food availability on the landscape, and may therefore act as a poor proxy for habitat suitability for the CRG. Our results suggest that understanding food availability across the landscape will be essential for identifying critical CRG habitat, and further studies will be needed to examine such availability and include non-herbaceous food items like fruit and bark.

An important limitation of this study is the incomplete list of included food species. While seasonal species, particularly fruit, are important to the CRG diet, we were unable to gather information on these species. While our results suggest the importance of food in CRG habitat use, we likely underestimate this importance, and we cannot detect patterns of how this importance may change across seasons. Thus, our results should be interpreted cautiously, and additional studies over multiple seasons and years will aid researchers in detecting the importance of various food species in CRG ranging patterns.

Another limitation of this study was the potential for misidentification of CRG nests, due to the difficulty in differentiating gorilla nests from chimpanzee nests. This may have led to the inclusion of chimpanzee nests unwittingly into the analysis, as well as exclusion of CRG nests if trackers could not agree on the nest source. When questionable chimpanzee sign were included as gorilla sign, the important food species *C. camerunensis* became significant at the subpopulation range, rather than within-range, scale and shrub understory became significant at the subpopulation scale. Other predictors remained the same. When older CRG sign were excluded from analyses, slope was maintained as a negative predictor of CRG presence within the subpopulation range, important food species shifted slightly at multiple scales (*C. camerunensis* became less significant, *Aframomum* sp dropped out and *Palisota* sp because more significant), and only human use, rather than both use and proximity to use remained significant at local scales. Other predictors remained the same. Thus, with inclusion/exclusion of potentially misidentified ape sign, the specifics of retained variables varied, but the general conclusions did not. The significant predictors retained in the best models at each scale – including topography, canopy closure, understory characteristics,

human use and food species availability – changed very little, suggesting robust study results. Nonetheless, a study of resource selection by chimpanzees in an area of the region might help researchers to better detect potential conflations.

As with most studies that apply RSFs, this study assumes that species occur most frequently in the most suitable habitat, which may not always be true (Dussault *et al.*, 2006; Hirzel & Le Lay, 2008). Additionally, model validation is a key component for assessing the utility of RSFs (Howes & Lougheed, 2004; Hirzel *et al.*, 2006; Johnson & Gillingham, 2008; Wiens *et al.*, 2008; Coe *et al.*, 2011), and challenging field conditions led to small sample sizes in our study, preventing us from independently validating our models. Finally, detection error affects reliability of RSFs (Boyce, 2006). Thus, expanding data collection over a longer time period, testing detection error rates, conducting model validation and using more direct measures of gorilla presence will greatly improve future study conclusions.

CONCLUSIONS AND FUTURE DIRECTIONS

This study highlights the utility of integration across multiple scales of resource selection to inform management strategies. A different picture of critical CRG habitat is presented with each progressively finer scale of resource selection, and together these scales produce a more complete understanding of relationships between species distribution and behaviour. When conservation planning relies on coarse-scale habitat models, it is essential that included variables do not mask finer-scale habitat selection decisions and trade-offs (Beier *et al.*, 2008; Sawyer *et al.*, 2011). Predictor variables that have direct ecological significance are always preferable to surrogate variables, which have only indirect association to causal factors but are often the only available data (Kirk & Zielinski, 2009). Our study suggests that both habitat type and distance from villages may be poor proxies for the landscape variables influencing CRG habitat use. Instead, conservation planning to ensure persistence of CRG subpopulations requires a closer look at staple food availability and human activities throughout the landscape to determine what proportion of remaining forest represents unsuitable vs. unoccupied habitat and to inform protection of critical habitat (Bergl *et al.*, 2012). The subtleties of sustainable and compatible human landscape uses are unclear and must be explored further. This study is limited in scope, and while a large-scale, data-intensive, multi-year study may be expensive and logistically difficult, it will prove crucial for gaining a deeper understanding of CRG niche ecology while informing habitat conservation planning in the region.

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SUPPORTING INFORMATION

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

Appendix S1 Additional detailed description of study methods.

BIOSKETCHES

Sarah C. Sawyer is a wildlife ecologist and conservation biologist. Her main interests are in habitat connectivity and suitability and their implications for conservation planning. Specifically, her research focuses on the biotic, abiotic and anthropogenic factors that affect habitat selection by wildlife species of conservation concern.

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