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RESEARCH ARTICLE

Informing Conservation Management About Structural Versus Functional Connectivity: A Case-Study of Cross River Gorillas

INAOYOM IMONG[1,2]*, MARTHA M. ROBBINS[1], ROGER MUNDRY[1], RICHARD BERGL[3], AND HJALMAR S. KÜHL[1]
[1]*Max Planck Institute for Evolutionary Anthropology, Leipzig, Germany*
[2]*Wildlife Conservation Society, Nigeria Program, Calabar, Cross River State, Nigeria*
[3]*North Carolina Zoological Park, Asheboro, North Carolina*

Connectivity among subpopulations is vital for the persistence of small and fragmented populations. For management interventions to be effective conservation planners have to make the critical distinction between structural connectivity (based on landscape structure) and functional connectivity (which considers both landscape structure and organism-specific behavioral attributes) which can differ considerably within a given context. We assessed spatial and temporal changes in structural and functional connectivity of the Cross River gorilla *Gorilla gorilla diehli* (CRG) population in a 12,000 km^2 landscape in the Nigeria-Cameroon border region over a 23-year period, comparing two periods: 1987–2000 and 2000–2010. Despite substantial forest connections between occupied areas, genetic evidence shows that only limited dispersal occurs among CRG subpopulations. We used remotely sensed land-cover data and simulated human pressure (using a spatially explicit agent-based model) to assess human impact on connectivity of the CRG population. We calculated cost-weighted distances between areas occupied by gorillas as measures of connectivity (structural based on land-cover only, functional based on both land-cover and simulated human pressure). Whereas structural connectivity decreased by 5% over the 23-year period, functional connectivity decreased by 11%, with both decreasing more during the latter compared to the earlier period. Our results highlight the increasing threat of isolation of CRG subpopulations due to human disturbance, and provide insight into how increasing human influence may lead to functional isolation of wildlife populations despite habitat continuity, a pressing and common issue in tropical Africa often not accounted for when deciding management interventions. In addition to quantifying threats to connectivity, our study provides crucial evidence for management authorities to identify actions that are more likely to be effective for conservation of species in human-dominated landscapes. Our approach can be easily applied to other species, regions, and scales. Am. J. Primatol. 76:978–988, 2014. © 2014 Wiley Periodicals, Inc.

Key words: connectivity; conservation; Cross River gorilla; fragmented landscapes; habitat; human pressure

INTRODUCTION

A major concern of conservation biologists and wildlife managers is the persistence of species in human-dominated landscapes [Chapin et al., 2000; Vitousek et al., 1997]. Due to human influence a rapidly increasing number of species including primates live in small, fragmented populations in human-dominated landscapes [Arroyo-Rodríguez & Dias, 2010; Coulon et al., 2004; Estrada et al., 2002; Haag et al., 2010; Hanski & Gaggiotti, 2004; Mittermeier et al., 2012] often confined to suboptimal refuge areas [Güthlin et al., 2011; Naves et al., 2003]. The long-term viability of such populations is threatened by loss of genetic diversity and reduced resilience to demographic and environmental stochasticity associated with reduced dispersal and small population size [Bergl et al., 2008; Caughley, 1994; Haag et al., 2010; Lande, 1993].

The critically endangered Cross River gorilla, *Gorilla gorilla diehli* (CRG), inhabiting the densely human populated Nigeria-Cameroon border region is

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*Correspondence to: Inaoyom Imong, Max Planck Institute for Evolutionary Anthropology, Deutscher Platz 6, 04103, Leipzig, Germany. E-mail: inaoyom_sunday@eva.mpg.de; iimong@wcs.org

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a good example. Fewer than 300 CRG were estimated to survive as of 2007, fragmented into approximately 14 small subpopulations restricted to small hilly areas covering ~600 km^2 across a landscape of ~12,000 km^2 [Bergl et al., 2012; Oates et al., 2007]. Although most CRG localities are connected by forest, dispersal among the subpopulations is limited [Bergl & Vigilant, 2007]. Given its small and fragmented distribution, a key objective of CRG conservation management is to maintain connectivity among subpopulations [Bergl & Vigilant, 2007; Bergl et al., 2008; Oates et al., 2003, 2007].

Connectivity is defined as "the degree to which the landscape facilitates or impedes movement among resource patches" [Taylor et al., 1993; Tischendorf & Fahrig, 2000], or "the functional relationship among habitat patches, owing to the spatial contagion of habitat and the movement responses of organisms to landscape structure" [Taylor et al., 1993; With et al., 1997]. Two types of connectivity are recognized: structural and functional [Kindlmann & Burel, 2008], and conservation management needs to consider both in order to develop effective interventions (e.g., habitat restoration versus management of ongoing human activities). Structural connectivity relates mainly to landscape structure without consideration of the behavioral attributes of organisms [Metzger & Decamps, 1997; Taylor et al., 1993]. Functional connectivity, on the other hand, considers both landscape structure and the behavioral responses of species to landscape elements, taking into account the quality of the habitat between the patches or populations of interest and the nature of the surrounding matrix into which organisms may venture [Kindlmann & Burel, 2008]. In hunted species for example, occurrence and dispersal may become limited despite availability of ecologically suitable habitat if mortality risk from hunting is high [Blake et al., 2008; Delibes et al., 2001; Hickey et al., 2013; Imong et al., 2013; Junker et al., 2012; Naves et al., 2003]. Failing to consider both types of connectivity may lead to erroneous assessment of threats and development of ineffective management strategies.

Assessing spatial and temporal patterns of functional connectivity can provide insights into potential future changes in population structure and guide development of effective management strategies [Coulon et al., 2004; Sharma et al., 2013]. Genetic methods provide information about population structure that can be used to infer levels of functional connectivity among fragmented populations [Bergl & Vigilant, 2007; Haag et al., 2010]. However, changes in population structure may occur over relatively long temporal scales and there is often a time-lag between landscape alteration due to land-use change and genetic change [Poissant et al., 2005]. An alternative method is to analyze changes in landscape structure and factors that influence the behavioral responses of target species that can be used to predict potential future changes in population structure, and therefore inform conservation planning and management to avert genetic consequences of population isolation.

The measurement and use of connectivity is context dependent [Tischendorf & Fahrig, 2000, 2001]. Different measures have been used to quantify functional connectivity including: (1) those based on the probability of organism movements between patches; and (2) those based on matrix permeability which assesses the resistance of landscape matrix using species-specific migration behavior information [Kindlmann & Burel, 2008]. The first type often require data on actual animal movements between patches and is therefore less applicable where such data are lacking as in the case of our study species. The second type, which we used in this study, can provide useful results for guiding conservation planning, especially when validated with observational or genetic data on actual dispersal [Driezen et al., 2007].

We assessed spatial and temporal changes in connectivity among CRG subpopulations over a period of 23 years from 1987 [when gorillas were "rediscovered" in Nigeria; Harcourt et al., 1989] to 2010, contrasting between structural and functional connectivity. We used remotely sensed land-cover data and simulated human pressure to assess human impact on connectivity of the CRG population. We simulated human pressure over the landscape using a spatially explicit agent-based model. An agent-based model (ABM) is a computational model for simulating the actions of autonomous agents (individual or collective entities) and their interactions with the environment aimed at assessing their effects on complex systems [Bonabeau, 2002]. ABMs are increasingly used to study spatial and temporal patterns of human land-use and their consequences on ecological systems [Bousquet et al., 2001; Brown et al., 2005; Manson & Evans, 2007; Matthews et al., 2007]. Using an ABM model allowed us to obtain additional information on human pressure to complement information from land-cover images. It also allowed us to better take into account human activities such as hunting and collection of other forest products that influence the ability of gorillas to disperse but are usually less detectable from satellite imagery, thus permitting a better understanding of threats to functional connectivity of the CRG population.

METHODS

Study Area

The study area covers ~12,000 km^2 in the mountainous southern border region between Nigeria and Cameroon (longitudes E 8.7°–10°E;

latitudes 5.6°–6.5°N) and included the entire range of CRG as of 2010 (Fig. 1). The area encompasses seven protected areas as well as large areas of unprotected community forest. The landscape is a mosaic of forest, farmland and human settlements. Habitat loss, alteration and fragmentation in the region result from agricultural conversion, logging, seasonal bush fires, road building, and other infrastructural development. Annual deforestation rate in some parts of the region was estimated at 2.7% between 1990 and 2000 and 3.7 between 2000 and 2010 [FAO, 2010]. Human population density in this region is among the highest in Africa, with some areas supporting as high as 500 people per km^2 [Oates et al., 2004]. The habitat is diverse, ranging from tropical lowland forest and mid-elevation forest to submontane and montane forest and grassland [Oates et al., 2003].

Cross River Gorilla Localities

Gorilla localities were defined using presence data from available records (including several unpublished reports of surveys conducted by the Wildlife Conservation Society) since 1987 [Bergl et al., 2012; Harcourt et al., 1989; Harris et al., 1987; Oates et al., 2003, 2004; Sunderland-Groves, 2008; Sunderland-Groves et al., 2003; Thomas, 1988]. The occupied range was estimated by applying a 1.5 km buffer to presence locations, and then manually editing it to exclude areas where gorillas were known to be absent (e.g., villages) and to include contiguous forested hilly areas [Bergl et al., 2012]. Three genetically distinct subpopulations (Fig. 1) are identified: a western subpopulation located in the Afi Mountain Wildlife Sanctuary in Nigeria, a central/transboundary subpopulation including most of the 14 localities, and an eastern subpopulation in the Kagwene Gorilla Sanctuary, Cameroon [Bergl & Vigilant, 2007].

Land-Cover and Topographic Data

We used satellite-derived land-cover data (spatial resolution: 30 × 30 m) obtained from the U.S. Geological Survey (https://earthexplorer.usgs.gov) to assess forest cover change. We obtained three Landsat scenes (corresponding to Worldwide Reference System path 187, row 056) of the years 1987 (TM; acquired January 29, 1987), 2000 (ETM+; acquired December 10, 2000) and 2010 (ETM+; acquired January 20, 2010) covering the entire range of CRG. The images were relatively free of clouds. All scenes were radiometrically and geometrically corrected at source with the Standard Terrain Correction (Level 1T; http://landsat.usgs.gov/products_productinformation.php). Scan Line Corrector (SLC-off) gaps in the 2010 image were partially filled using the TERAS method in PANCROMA (version 5.16). The images were classified using supervised classification and the Maximum Likelihood classifier in

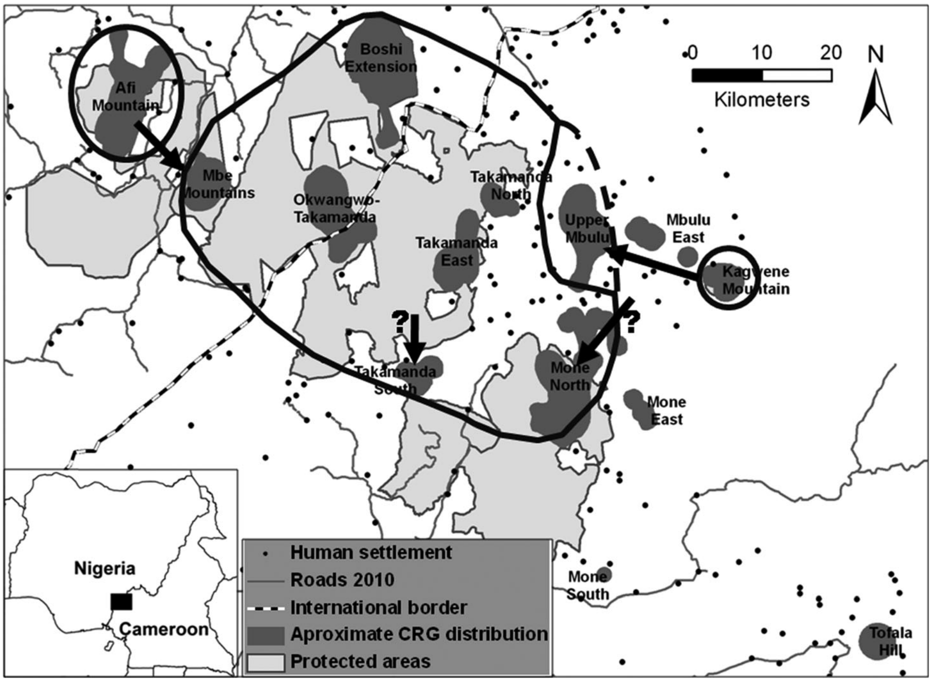

Fig. 1. Map of the study area in the border region between Nigeria and Cameroon (insert) showing approximate distribution of Cross River gorillas, protected areas, roads, and human settlements. Shown (black polygon and circles) are the three “genetic populations” [Bergl & Vigilant, 2007], and the location of migration events as deduced from DNA evidence (arrows). The origins of the migrants into the Takamanda South and Mone North localities are uncertain. Adapted from Oates et al. [2007].

IDRISI (Idrisi32 Release 2). We identified six land-cover categories which we condensed to four classes: "forest," "disturbed forest and farmland," "grassland and low vegetation," and "bare earth" (including human settlements) for subsequent analyses. Other habitat types not included in the four above (covering ca. 0.02% of the study area) were excluded from the analysis. We determined the area forest in each classified image using the area calculation tool in IDRISI. We obtained topographical data from the Shuttle Radar Topography Mission Digital Elevation Model (90 m resolution) (SRTM DEM; USGS, 2004). These data were used to create a slope surface, which we used in the estimation of accessibility of grid cells in the landscape.

Classification Accuracy Assessment

We assessed classification accuracy using ERRMAT tool in IDRISI. For the 2010 classification we used 358 ground-truth points obtained in the field in 2010 and 332 locations extracted from high-resolution imagery of 2009 (Geoeye: 2 m and Ikonos: 1 m) available for parts of the study area. We assessed accuracy of the 2000 classification by comparing 288 locations with a classification of a 2003 Landsat image for which ground-truth points obtained in the field were available in the same year [Bergl et al., 2012]. Accuracy of the 1987 classification was assessed by comparing 90 locations on the classified image with corresponding locations on a forest cover map of 1994 [Government of Nigeria, 1994]. Accuracy assessment of the 1987 classification was based on the two land-cover categories identified in the 1994 forest cover map: forest and non-forest. Overall accuracy of our classification was high (Table I).

TABLE I. Results of Accuracy Assessment of Land-Cover Classification, as Percentage of Points Correctly Classified

Mapped land-cover	Ground-truthed land-cover				Overall KIA
	MF	GL/LV	BE/HS	DF/FL	
2000					
MF	97.6	0.5	0	1.9	89
GL/LV	7.9	89.5	0	2.6	
BE/HS	0	0	100.0	0	
DF/FL	4.9	4.9	2.4	87.8	
2010	98.4	0	0.4	1.2	92
GL/LV	0	100.0	0	0	
BE/HS	4.2	0	95.8	0	
DF/FL	7.4	0	0	92.6	
1987	Forest	Non-forest			80
Forest	92.5	7.5			
Non-forest	8.7	91.3			

MF, mature forest; GL/LV, grassland and low vegetation; BE/HS, bare earth and human settlement; DF/FL, disturbed forest and farmland; KIA, Kappa index of agreement.

Human Population and Roads

Baseline human population data were obtained from national population census records of Nigeria and Cameroon (National Population Commission of Nigeria; National Office for Population and Housing Census of Cameroon). We projected baseline figures (Nigeria: 1991; Cameroon: 1987) to later years (2000 and 2010 when no censuses were conducted) using annual national population growth rates of the respective countries extracted from World Bank database (http://data.worldbank.org/indicator/SP.POP.GROW). We used the formula:

$$p_{\mathrm{t}} = p_{\mathrm{o}}(1+r)^{t}$$

where p_{o} is the basal population of the area (i.e., population for the years 1987 and 1991 for Cameroon and Nigeria, respectively); p_t is the projected population t years later; t is the time interval in calendar years between p_{o} and p_{t}; r is the growth rate of the population per year, assumed to remain constant over the time interval, t. We based the projections on the 1987 and 1991 figures because they were considered more reliable compared to figures from more recent censuses. To create GIS layers of roads, we manually digitized roads from satellite images for the three time periods (guided by personal knowledge of the study area). We included in the definition of roads a track that is usable by vehicles at least seasonally.

Agent-Based Simulation of Human Pressure

We simulated human pressure in the area for the three time periods from the locations of villages, their respective number of inhabitants, and the density of roads using a spatially explicit agent-based model based on a set of assumptions [Brown et al., 2005; Matthews et al., 2007]. We assumed that a higher density of humans would have a greater impact on the surrounding gorilla habitat, and the impact would vary with distance from human settlement and accessibility of the landscape (topography and density of roads). These factors are known to influence intensity of hunting and other human activities [Kuehl et al., 2009; Oates et al., 2003, 2007]. We simulated agents (humans including hunters, NTFP collectors, and other forest users) moving into the surroundings of their villages, with the number of agents per village being equal to the total number of inhabitants.

Agents moved across the landscape following a probabilistic random walk according to three rules. First, likelihood of agents moving out of their current location (a cell sized ca. 180 × 180 m of the simulated landscape) was proportional to the total number of agents in the cell. Second, agents could move in each of the eight cells directly adjacent to their current cell where the probability to move in any one of the eight cells was determined as the product of two values: the relative accessibility (i.e., slope steepness) of the cells, and the a preference matrix determined from the distances of the cells from the agent's village of origin. In addition, considering that roads facilitate access to remote areas, whenever a road passed through any of the eight cells we set the accessibility of the remaining cells to values such that their summed accessibility was 0.5, whereas that of the cell with a road passing through was set to one. The third rule related to the direction of movement with the cell to move into depending on whether an agent was moving away from or returning to its village of origin. When agents left their village of origin they were assigned a distance from their village they would need to reach before returning. These distances were randomly chosen from a normal distribution with a mean of zero and a standard deviation of 10 km, chosen based on the assumption that a majority (ca. 70%) of the human activity originating from villages happens within ca. 10 km distance from them [Etiendem et al., 2013; Imong et al., 2013]. When agents on their way home reached within three cells of their village of origin (540 m) they turned their direction and headed back to the cell containing the village. We ran the model 5,000 time steps for each of the three periods using the respective estimated human population size.

Cost-Weighted (Functional) Distance Calculation to Estimate Connectivity

We adopted a cost-weighted distance approach to assessing connectivity [Drielsma & Ferrier, 2009; Drielsma et al., 2007]. We measured cost-weighted distance [a GIS raster function that measures the cumulative cost of moving through grid cells in a landscape; Petit & Burel, 1998] between areas occupied by gorillas as a measure of connectivity of the CRG subpopulations. The cost-weighted distance approach takes into account heterogeneous habitat in the landscape between resource patches or populations in contrast to Euclidean (linear) distance assuming a homogeneous landscape. Cost-weighted distances were calculated for each of the three time periods.

To calculate cost-weighted distances we created two "permeability" matrices, one based on human pressure, the other on habitat type (ranked according to known habitat preferences of Cross River gorillas: forest, disturbed forest and farmland, grassland and low vegetation, and bare earth including human settlement). Both matrices were standardized to values theoretically ranging from zero to one, with one representing maximum permeability of cells for gorillas to move through and zero representing minimum permeability. However, the standardization was conducted such that values in the matrices for the three time periods remained comparable. To keep computation time reasonable we decreased the resolution of the original maps (human pressure: 180 × 180 m; habitat: 30 × 30 m) to ca. 920 m by averaging cells. This cell size was considered appropriate because it falls within the range of daily travel distance of CRG [McFarland, 2007]. Further, we squared the entries in both maps to account for the potentially larger effect of a change in permeability for cells with larger permeability values compared to cells with smaller values (e.g., in a cell with few humans, the addition of one human more would have a larger effect than the addition of one human more in a cell in which there are already many humans).

For structural connectivity we calculated cost-weighted distances using the permeability matrix derived from land-cover only. For functional connectivity we combined the two permeability matrices (habitat type and human pressure) by multiplying them. By incorporating the simulated human pressure we took into account human activities that impact gorilla survival and dispersal, but do not significantly alter vegetation structure and therefore are not adequately detected through remote sensing analysis (e.g., hunting and collection of other NTFPs). Based on the cost-weighted distances we estimated structural and functional connectivity between pairs of occupied areas for the three time periods, whereby we took the median of the shortest distances per pair as the final distance between them, and compared changes during two periods: 1987–2000 and 2000–2010 using Friedman test.

Implementation of Models

The agent-based model, processing of maps and cost-weighted distance calculations were implemented in R [version 2.14.1; R Development Core Team, 2011]. Reading of geographical shapefiles was done using the Read and Write ESRI Shapefiles package [Stabler, 2006]. Cost-weighted distances were derived using the function costDistance of the package gdistance [van Etten, 2011] and parallelized using the R package parallel [R Development Core Team, 2011].

RESEARCH ETHICS

All work conformed to research regulations of Nigeria and Cameroon and adhered to the American Society of Primatologists (ASP) principles for the ethical treatment of non-human primates.

RESULTS

Forest Cover Change

Remote sensing analysis showed that during the analysis period 66–76% of the study area was forest. The rate of forest loss was lower during 1987–2000

TABLE II. Total Forest Area and Forest Loss in the CRG Landscape During the 23-Year Period From 1987 to 2010

Period	Total forest area (km^2)	% of study area
1987	9,091	76
2000	8,884	74
2010	7,927	66
Period	Total forest loss (km^2)	% loss
1987–2000	207	2.3
2000–2010	957	10.8
1987–2010	1,164	12.8
Period	Human population increase (%)	
1987–2000	29	
2000–2010	33	
1987–2010	71	

(2.3%) as compared to during 2000–2010 (10.8%) when forest loss accelerated rapidly (Table II; Fig. 2), corresponding to an increase in human population and road density during this period.

Spatial and Temporal Patterns of Connectivity Between CRG Localities

Overall, connectivity of the CRG habitat decreased during the 23 years period (Fig. 3, Table III; Friedman test, functional: $\chi^2 = 24.13$, df = 2, $P < 0.001$; structural: $\chi^2 = 19.6$, df = 2, $P < 0.001$) but to a greater extent in the 2000–2010 period compared to 1987–2000. We also found a greater decrease in functional connectivity (influenced by both forest cover and human disturbance) compared to structural connectivity (estimated based only on land-cover) in the 2000–2010 period (Fig. 3; Table III).

Functional distances were relatively short between many subpopulations including Afi–Mbe, Mbe–Okwangwo–Takamanda, and among subpopulations within and around Takamanda, Mone, Mbulu, and Kagwene, suggesting that there was potential for migration. However, functional distances between other subpopulations were large, suggesting low potential for migration between them (Fig. 4; Table IV). Three subpopulations: Boshi Extension, Tofala, and South Mone were the least functionally connected to other subpopulations and considered most at risk of isolation (Fig. 4; Table IV). Although Euclidean distance between the Boshi Extension subpopulation and other subpopulations is relatively short (Table IV), it had the longest cost-weighted distance to other subpopulations making it more threatened with isolation than previously thought. Some subpopulations previously considered well connected based on forest cover (e.g., Mbe–Okwangwo–Takamanda and Okwangwo–Takamanda–Takamanda East) were found to be functionally not so well connected, with functional distances between these populations increasing rapidly (Table IV).

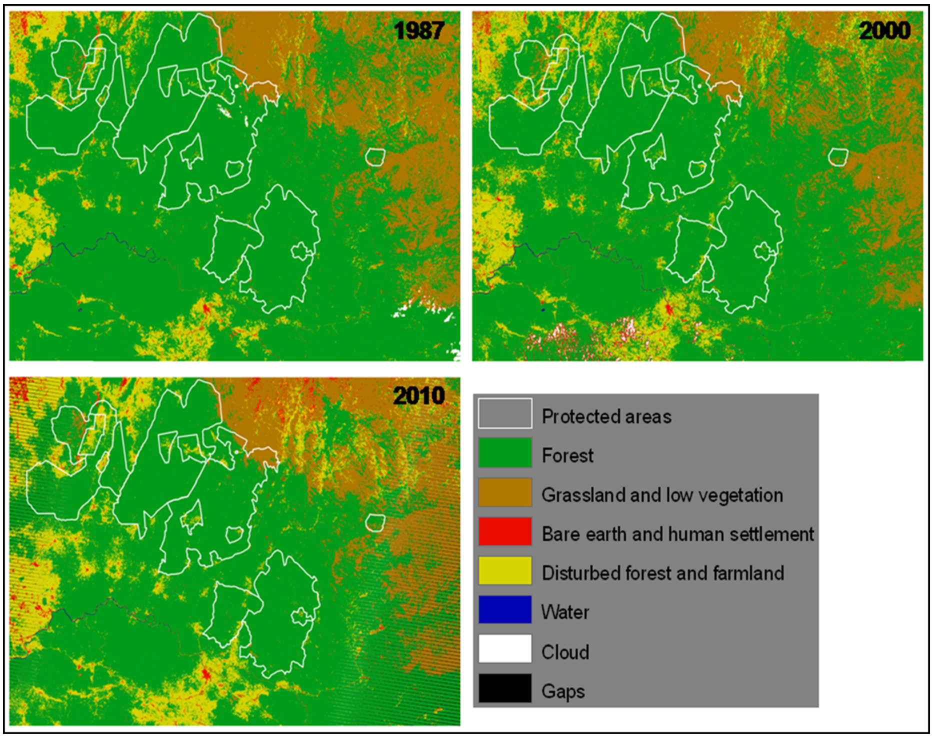

Fig. 2. Land-cover in the study area in 1987, 2000, and 2010 based on classified Landsat images.

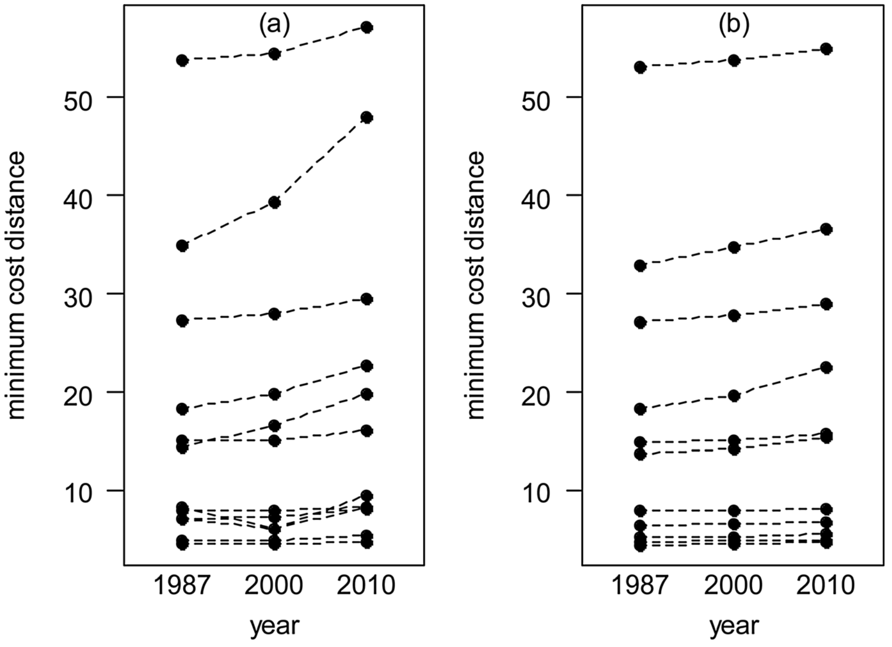

Fig. 3. Cost-weighted distances between subpopulations (shortest paths) for three periods: 1987, 2000, and 2010; (**a**) functional, (**b**) structural.

DISCUSSION

We found that although most CRG subpopulations remained well connected to at least one other subpopulation by forest, dispersal among some subpopulations was threatened by increasing human disturbance. The rapid decrease in functional connectivity in the latter period of our analysis (2000–2010) compared to the earlier period (1987 and 2000) indicates increasing threat to the ability of CRG to disperse across their range. Our results highlight both the challenges and opportunities for CRG conservation. While the existence of substantial habitat linkages and corridors between areas of occurrence represent potential for dispersal among population fragments, increasing human pressure from hunting and collection of other forest products threatens dispersal and consequently long-term persistence of the population [Bergl et al., 2012; Fa et al., 2006; Imong et al., 2013; Oates et al., 2003].

TABLE III. Median Percent Change in Functional Connectivity of the CRG Population During Two Periods (1987–2000 and 2000–2010)

	Median % connectivity change	
Period	Functional	Structural
1987–2000	2.49	2.43
2000–2010	11.56	3.91
1987–2010	10.95	5.35

Our study shows that structural and functional connectivity can differ considerably within a given context and that failing to distinguish between the two and to consider both aspects of connectivity may lead to erroneous assessments of threats and the development of ineffective conservation interventions. It further suggests that under high human influence wildlife populations may become fragmented and functionally isolated even when substantial ecologically suitable habitat remains within the landscapes they occupy [Hickey et al., 2013; Imong et al., 2013], a situation that requires greater attention in conservation planning and management. This is evident from the relatively high functional distances between some localities where human disturbance was high, though structurally well connected. By contrasting structural and functional connectivity spatially and temporarily our study provides crucial evidence to inform conservation management about which actions will be more effective (e.g., reducing ongoing human activities such as hunting and collection of other forest products and relocating enclave communities from connectivity areas would be more effective than restoration of vegetation).

Our results are supported by genetic evidence of recent migration between some CRG subpopulations [Bergl & Vigilant, 2007]. All localities where migration was detected through genetic analysis were found to have among the shortest functional distances to other subpopulations in our study (Table IV; Fig. 4). These include Afi (previously considered the second most threatened with isolation after the

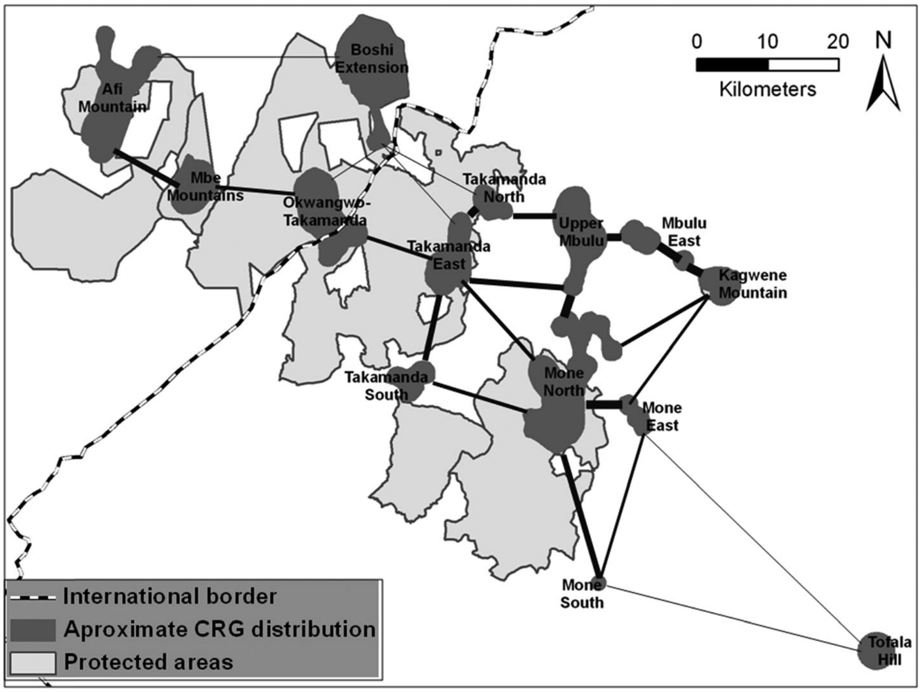

Fig. 4. Functional connectivity (dark lines) between pairs of CRG localities. Line width represents strength of connectivity.

TABLE IV. Euclidean and Cost-Weighted Distances Between CRG Localities and Temporal Changes

Localities	Euc. dist. (km)	1987	2000	2010	1987–2000	2000–2010
E. Mbulu–E. Mbulu	2	8.5	8.7	10.2	−0.2	−1.5
Kagwene–E. Mbulu	**1**	**9.8**	**7.4**	**11.4**	**2.4**	**−4.0**
N. Mone–Upper Mbulu	**2**	**10.2**	**10.3**	**11.0**	**−0.1**	**−0.7**
E. Takamanda–N. Takamanda	1	11.1	11.2	11.8	−0.1	−0.6
E. Mone–N. Mone	3	12.5	12.4	13.1	0.1	−0.6
E. Mbulu–Upper Mbulu	2	12.7	12.1	14.1	0.6	−2.1
N. Takamanda–Upper Mbulu	6	13.9	14.2	15.4	−0.3	−1.2
E. Takamanda–S. Takamanda	**9**	**19.1**	**19.4**	**20.5**	**−0.3**	**−1.1**
Afi–Mbe	**8**	**20.4**	**24.0**	**27.1**	**−3.6**	**−3.1**
E. Takamanda–Upper Mbulu	11	20.6	20.9	22.0	−0.3	−1.2
S. Takamanda–N. Mone	11	23.1	23.6	24.7	−0.5	−1.0
Mbe–Okwangwo	10	25.9	28.1	32.7	−2.3	−4.6
Okwangwo–E. Takamanda	9	26.2	30.6	48.1	−4.5	−17.5
E. Takamanda–N. Mone	13	26.3	26.7	27.4	−0.4	−0.8
Kagwene–N. Mone	13	30.4	28.7	32.8	1.7	−4.1
S. Mone–N. Mone	17	31.9	32.6	34.3	−0.7	−1.7
S. Mone–E. Mone	20	32.5	33.3	34.5	−0.8	−1.3
Kagwene–E. Mone	18	35.5	32.1	38.6	3.4	−6.6
Boshi Extension–E. Takamanda	13	42.6	47.0	56.7	−4.4	−9.7
Boshi Extension–N. Takamanda	13	42.8	47.2	57.5	−4.4	−10.3
S. Mone–Tofala	37	54.9	55.5	58.3	−0.6	−2.8
Okwangwo–Boshi Extension	10	59.2	73.2	99.4	−14.0	−26.2
Afi–Boshi Extension	25	63.8	63.2	64.0	0.6	−0.8
E. Mone–Tofala	42	70.0	69.2	73.6	0.8	−4.4

Subpopulations between which migration was detected or suspected through genetic analysis are in bold (2nd, 3rd, 8th, and 9th rows).

Tofala subpopulation, which is also furthest by Euclidean distance), Mbe, Kagwene, Upper Mbulu, Takamanda East, Takamanda South, and Mone North (Table IV; Fig. 4). Furthermore, some structurally close subpopulations (in terms of forest cover and linear distance) such as Mbe–Okwangwo, Okwangwo–Takamanda East, and Boshi Extension–Okwangwo, between which migration was not detected through genetic analysis [Bergl & Vigilant, 2007], were found to have the least functionally connectivity in our study (Table IV; Fig. 4). Our analysis showed that the Boshi Extension population was more threatened with isolation than previously thought. Although connectivity of the Boshi Extension subpopulation was known to be threatened by the expanding enclave communities within the Cross River National Park and a number of surrounding villages, it seems from our study that the magnitude of threat may have been underestimated. Our results support the recommendation of the 2007 Action Plan [Oates et al., 2007] to seek long-term solutions to the issue of expanding enclave communities within protected areas in the CRG range, including possible relocation of such communities to areas where their impact on connectivity would be reduced.

Based on the increasing isolation of the Boshi Extension, South Mone, and Tofala subpopulations it is possible that they could become genetically isolated in the future, thereby altering the current three-cluster population structure [Bergl & Vigilant, 2007] to a more fragmented one. Our study highlights the utility of landscape connectivity analysis, which is much faster and cheaper than genetic analysis, for gaining insights into threats to connectivity of populations in fragmented landscapes that could inform conservation planning to mitigate potential negative consequences of small populations in the future.

A constraint to accurate analysis of connectivity for fragmented populations of wide-ranging threatened species is the scarcity of detailed data on human activities that directly impact their survival, such as hunting and other human disturbance over large spatial scales. In this study, we dealt with this problem by employing spatially explicit agent-based modeling to simulate human pressure (a proxy for intensity of hunting and other human disturbance), thereby complementing traditional satellite-derived land-cover data. We believe that this approach allowed us to better account for hunting pressure and other human activities that are less detectable from satellite imagery, and therefore permitted a clearer understanding of threats to functional connectivity of the CRG population. Accounting for the influence of hunting pressure in the analysis of connectivity is particularly useful in tropical forests environments where over hunting has depleted wildlife (especially large mammals) in many areas of otherwise intact forest—that is, the "empty forest syndrome" [Harrison, 2011; Redford, 1992; Redford & Feinsinger, 2001; Wilkie et al., 2011].

A limitation of our agent-based model is that it was based on the assumption of a linear relationship between human population density, road density and hunting pressure, although the exact relationship may be influenced by other socioeconomic factors [Shibia, 2010; Shrestha & Alavalapati, 2006]. However, several studies have shown that hunting pressure correlates positively with human population and road density [Blake et al., 2008; Harcourt et al., 2001; Kuehl et al., 2009; Laurance et al., 2006; Maisels et al., 2013; Muchaal & Ngandjui, 1999; Remis & Jost Robinson, 2012; Wilkie et al., 2000; Yackulic et al., 2011].

Conservation and Management Implications

Our results highlight the importance of considering both structural and functional connectivity for understanding threats to meta-population dynamics and for developing management strategies. In the case of CRG, functional connectivity is decreasing despite substantial forest connections between many subpopulations. Management therefore needs to focus on reducing human disturbance from hunting and collection of other NTFPs in corridor areas to improve functional connectivity. With many movement corridors located in areas with no formal protection, a landscape-based approach with greater management intervention in unprotected corridor areas is essential. The need for a landscape-based approach (as opposed to a site-based approach) to CRG conservation is recognized [Oates et al., 2007]. This approach has been adopted since 2007 and has led to increased conservation intervention (including creating greater conservation awareness and increasing community participation) in unprotected habitat areas across the CRG landscape, in addition to law enforcement within protected areas and should therefore be maintained. Increased conservation awareness and community participation in conservation are essential actions for effective CRG conservation [Oates et al., 2007]. The landscape-based approach to conservation has been applied in other regions and considered to be effective. Examples include the Congo Basin Forest Partnership landscapes in the Central African region [Stokes et al., 2010; Yanggen et al., 2010] and the WCS Andes Conservation Program Landscapes in the Amazon region [Painter et al., 2008]. Furthermore, systematic landscape-wide monitoring of human activities in corridor areas should be implemented to directly measure the success of interventions.

Although we focused on a single species and landscape, our study has clear implications for conservation management of a wide range of species and landscapes. We believe that our results reflect the situation in many other increasingly human-dominated landscapes, particularly in tropical Africa where the threat to wildlife is increasing rapidly as human population and access to remote areas increase [Blake et al., 2008; Laurance et al., 2006; Maisels et al., 2013; Remis & Jost Robinson, 2012; Wilkie et al., 2000; Yackulic et al., 2011]. Our approach can be easily replicated with other species or regions and across different spatial scales.

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