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African apes coexisting with logging: Comparing chimpanzee (*Pan troglodytes troglodytes*) and gorilla (*Gorilla gorilla gorilla*) resource needs and responses to forestry activities

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ABSTRACT

The extraction of timber often conflicts with the well-being and conservation of wildlife. In particular, there is a need to better understand the impact of tree removal under selective logging regimes on local ecological communities. We conducted ape nest counts along line transects before, during, and after logging to assess the impact of timber harvesting and associated activities on sympatric chimpanzees and gorillas in a forestry concession in northern Republic of Congo. We used generalized linear models to relate ape nest counts to a set of predictor variables, representing the impact of logging and controlled for variation in environmental conditions including food availability, habitat and rainfall. Commercial forest inventory data were used to assess the baseline influence of food availability and forest structure on ape distribution. Higher numbers of chimpanzees were found in proximity to their preferred tree foods, whereas gorillas were associated with more heterogeneous habitats. Chimpanzee nest encounter rates decreased with increasing intensity of human impacts. Gorillas also avoided areas with active timber exploitation and roads, but were attracted to recently logged areas with abundant terrestrial herbaceous vegetation. Species-specific responses were consistent with theoretical predictions of niche partitioning and cumulative human influence. Based on these findings, we provide recommendations to improve existing guidelines and forest certification standards aimed at safeguarding ape populations.

1. Introduction

Among the anthropogenic influences on environmental services and biodiversity in the tropics, timber exploitation plays a prominent and complex role (Asner et al., 2010; Barlow et al., 2016; Brandt et al., 2016; Nasi et al., 2012). Rates of ecosystem conversion have increased and become more widespread (Gibbs et al., 2010; Hansen et al., 2013) with roughly 20% of the tropical forest worldwide having been subjected to selective logging at the turn of the century (Asner et al., 2009). Logging can provide important revenue streams and opportunities for infrastructure development in some of the most disenfranchised regions of the world (FAO, 2011), but these benefits have costs with regards to tropical forest health (Lewis et al., 2015) and conservation of biodiversity. The advent of sustainable forest management (SFM) provides counter measures to alleviate potential negative impacts on the environment (see review by Putz et al., 2008) characterizing selectively logged forest as "middle way" toward maintaining biodiversity (Putz et al., 2012).

Most of the timber estate in the Congo Basin has already experienced one or two cycles of exploitation (Perez et al., 2005). As a result, the floral composition and structure of these production forests are under transition. Forest conversion can have neutral, beneficial or

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detrimental effects on wildlife depending on species-specific traits and coping mechanisms (Burivalova et al., 2014). Within converted landscapes, the distribution of wildlife is likely to be altered and understanding the risks to particular species is key to their conservation. Life history traits such as niche breadth and habitat specificity are a few factors linked to species sensitivity to anthropogenic impacts (Henle et al., 2004). The response of sympatric western gorilla and central chimpanzee to anthropogenic impacts are of interest given these species subtle differences in resource use and social systems.

Gorillas have classically been referred to as generalists belonging to the folivore guild (consuming mostly herbaceous ground vegetation) and chimpanzees as specialists grouped within the frugivore guild (consuming mostly fruit) (Bourliere, 1985). Based on these differences in their ecological profiles, scientists have suggested that chimpanzees are expected to be more negatively impacted by human impacts. Prior studies partially supported such assertions, with decreases in chimpanzee populations after a first cycle of selective logging (Arnhem et al., 2008; Clark et al., 2012; White and Tutin, 2001). In contrast, gorilla numbers remained similar or increased in some exploited forests (Haurez et al., 2014; Huijbregts et al., 2003).

Both species are wide ranging and capable of identifying refugia to avoid areas with active timber harvesting but they differ in social constraints to shifting their ranging patterns. Home ranges of gorilla groups may overlap completely without dispute. Tolerance may afford the opportunity for gorillas to spatially shift their ranges to avoid localities with high levels of human impact (Arnhem et al., 2008; Matthews and Matthews, 2004), as has been observed in Bornean orangutans living in proximity to logging (Ancrenaz et al., 2004; Davies, 1986; MacKinnon, 1971; Morrogh-Bernard et al., 2003; Russon et al., 2001). In contrast, chimpanzees are territorial and aggressively defend resources in their home range from incursions by neighboring groups, which limits their ability to shift spatially (Goodall, 1986; Mitani et al., 2010). In Gabon, an immediate and significant decline of chimpanzees occurred after the onset of timber exploitation, which was attributed to lethal conflicts between neighboring groups as they were displaced from their territories by logging (White, 1994; White and Tutin, 2001). There have been few studies of apes' responses to logging that integrate ecological and anthropogenic factors, habitat selection, and potential ecological trade-offs (Haurez et al., 2016; Imong et al., 2014; Sawyer and Brashares, 2013). Though similar approaches have proven informative outside of the Congo Basin in different anthropogenic contexts (Hardus et al., 2012; Henle et al., 2004; Hockings et al., 2009; Felton et al., 2003; Felton et al., 2010; Melbourne et al., 2004; Rode et al., 2006; Potts, 2011).

To assess the impact of selective logging on the ape guild, we conducted ape nest counts over a nine-year period along standardized line transects using a before, during and after (BDA) methodology. The potential influence of forest structure and food availability on ape distributions was estimated with commercial timber inventory (CTI) data from the study area. Based on their ecological and social profiles, we hypothesized that chimpanzees and gorillas would show different responses to logging activity. We predicted that chimpanzees would avoid areas of active exploitation through small-scale spatial shifts. Gorillas were also predicted to avoid zones of high human impact, but through larger spatial shifts resulting in convergence in secondary habitats comprised of their preferred food resources. We used Generalized Linear Models to relate chimpanzee and gorilla nest counts to a set of predictor variables, representing the impact of logging and controlled at the same time for variation in environmental conditions including food availability, habitat, and rainfall. Given the potential long-term risks that logging poses to their survival, conservation priorities at the concession level need to be based on the resource needs of these critically endangered gorillas and endangered chimpanzees (IUCN, 2016).

2. Methods

2.1. Study site

The study was conducted in the Kabo Forestry Management Unit, the first Forest Stewardship Council (FSC) certified concession in central Africa. The concession is adjacent to the Nouabalé-Ndoki National Park (NNNP) (2°05′–3°03′N; 16°51′–16°56′E) in northern Republic of Congo. The area had been logged 30 years ago, but timber extraction was selective and many of the largest tree stems were left intact. Our baseline ape density estimates were within the range of those found in neighboring pristine forests, and botanical inventories suggested that natural forest recovery was underway and preferred ape foods available (Morgan unpublished data). Altitude within these lowland forests ranged from 330 to 600 m. The climate can be described as transitional between the Congo-equatorial and sub-equatorial climatic zones.

2.2. Study design and data collection

We used the automated survey design component of the custom DISTANCE software to generate systematically spaced line transects with a random start in the study area (Thomas et al., 2010). Results from a line transect pilot study indicated that a survey design comprised of fourteen parallel line transects separated by 1.5 km would provide sufficient survey effort for the desired precision. This systematic design ensured that each location in the study area had the same probability of being sampled (Fig. 1).

Line transects were surveyed twelve times between 2004 and 2012, and conducted in adherence to best practice guidelines for surveys and monitoring of great ape populations (Kühl et al., 2008). The first passage was conducted in 2004, before the current timber harvesting began in 2006. Surveys were conducted twice a year while active logging took place in the study area between 2006 and 2009 (8 times). Post-logging surveys were conducted between 2010 and 2012 (3 times). Ape nests and human signs were recorded on each survey passage. See Morgan et al. (2006) for a detailed description of data collection protocols and methods.

2.3. Timber inventory data

An agreement between the local logging company, the Wildlife Conservation Society (WCS), and the Government of Congo was signed in 1999 to ensure environmental and social values were maintained within the production forests. As part of concession management planning in central Africa (Cerutti et al., 2008) and FSC certification, the local logging company, in collaboration with the Government of Congo, conducted a commercial timber inventory (CTI) prior to initiation of timber removal. Similar studies focused on flora traits using CTI datasets have proven reliable (Réjou-Méchain et al., 2011) at a variety of spatial scales and improved understanding of the ecological characteristics of production forests (ter Steege, 1998; Réjou-Méchain et al., 2008). The georeferenced CTI for this study zone was conducted in 2003 and included tree stems with minimum diameter of exploitation ranging between 60 and 100 cm at breast height (DBH) depending upon species (Congolaise Industrielle des Bois, 2006). The spatially explicit inventory of individual trees surveyed in the study zone included stems from 40 different species of marketable and non-marketable trees. Nearly 90% of the timber volume removed was comprised of *Triplochiton scleroxylon*, *Milicia excelsa*, *Entandrophragma cylindricum*, and *E. utile* (Congolaise Industrielle des Bois, 2006). Annual Allowable Cut (AAC) areas were spatially defined based on the volume of timber approved for removal occurring within the region to be exploited. Delimitation of AAC areas and road construction occurred in advance of timber exploitation. As part of the third party certification, the logging company was audited once a year with auditors making field visits to the concession and interacting directly with the forestry company's

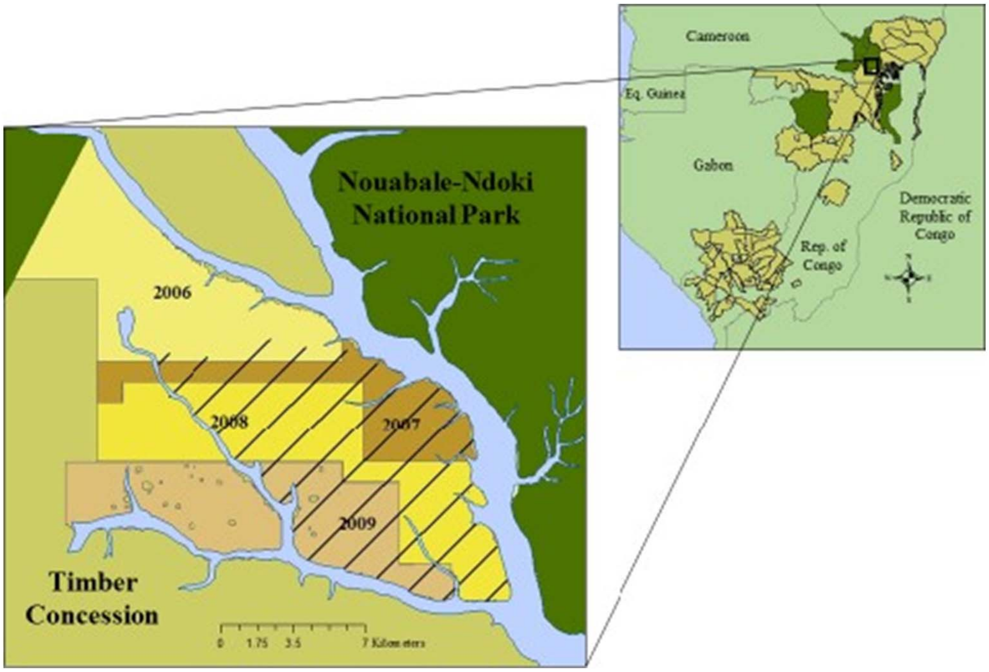

Fig. 1. Active logging concessions within the Republic of Congo including the Kabo concession and the study area. Transects (diagonal lines) were placed roughly perpendicular to waterways that bordered the zone of interest. Logging progressed within the study area roughly from northwest to southeast and occurred from 2006 to 2009 as indicated by the location of Annual Allowable Cut (AAC) units, highlighted in a different color for each year.

Director of Environment and Social Services and non-governmental partners, including independent scientists responsible for monitoring wildlife within the concession.

2.4. Ape nesting and feeding preferences

Ape nesting tree preferences were based on line transect surveys (Buckland et al., 2001) of ape nests conducted in the Goualougo Triangle study area, which is an area of intact forest that was part of the Kabo Forestry Management Unit until 2012 when it was annexed to the NNNP. Ape food preferences were determined separately for chimpanzees and gorillas and according to three different approaches. First, ape food preferences were based on direct observations of feeding events by chimpanzees and gorillas, feeding signs encountered while following the apes, and fecal analysis in the Goualougo Triangle study area from 1999 to 2014. The frequency of consumption of each food item served as the basis for our assessment of feeding importance of tree species for gorillas and chimpanzees. The respective feeding preference score (thereafter ‘absolute feeding preference’) was then simply the number of times the respective food was observed to be fed on. Second, we examined ‘relative feeding preference’ by weighting feeding observations by tree species densities (Morgan unpublished data). To avoid bias associated with sampling methods used for assessing feeding preference (for example, dietary assessment by fecal analysis is biased toward plant species whose seeds pass intact through the gastrointestinal tract of apes), our third approach involved testing a model with food preferences based on expert opinion (assessment by DM and CS). This involved assigning a rank to each tree species based on our overall understanding of the biological importance of tree species in ape diets or nesting behavior based on multiple years of ape field studies in this region. To determine nesting tree preferences (separately for chimpanzees and gorillas) we proceeded as for relative feeding tree preference. For the feeding and nesting trees preference scores see Table S1.

2.5. Human impacts

A variety of human signs were encountered during line transect surveys. The potential impact of each type of human sign likely differed, and hence we weighted them according to their presumed impact on great apes. Some types of human signs may be perceived as having a relatively large impact, e.g., a logging camp, while others may have a relatively small impact, e.g., a machete cut. Similarly, we assumed that the distance decay of this perception varies among the types of human signs, such that some impacts will be experienced farther away compared to others, which would have a very local affect. Based on potential impact and disturbance distance, we assigned an impact score between 1 (lowest impact) and 10 (highest impact) to each type of human sign (Table S2). Weighted impact scores were summed for each transect segment.

2.6. Data processing

First, we split the transects into segments of a length as close as possible to 1,000 m (range of segment lengths: 855 to 1,056 m). The segment length was selected to achieve reasonable spatial resolution (shorter segments) while avoiding too many segments with no nest observations (longer segments). The chosen length resulted in rather balanced distributions of the number of nests per segment (i.e., not too many zero nest counts, no very large nest counts; see appendix Fig. S1). Since nest surveys took place repeatedly this lead to an overall sample size of 1,056 combinations of segments and survey passage. For each segment, we determined a variety of predictor variables (used in our models), which characterized the degree of human impact and logging per segment, properties of the forest in the vicinity of the segments, and several other features for which we aimed to control. We chose 12 test predictor variables and 4 control variables (Mundry, 2014) representing the categories: human impacts, ape resources, vegetation, and climate to model the impact of forestry (see Table 1 for definitions of the predictors). Of these variables we considered four (bef.dur.aft, sqrt.dist.to.routes, distance.to.logging.filled, and sqrt.weighted.human.impact.per.km) to characterize the direct and immediate impact of logging, two (sqrt.tot.feed.tree.value.per.km, sqrt.tot.nest.tree.value.per.km) to represent the potential impact on important resources, and further six (tree.shannon, tree.contagion.1, sqrt.tree.same.neighbor.prob, tree.biomass, log.tree.biomass.cv, tree.size.biom.heterogeneity) to represent structural features of the habitat that might change as a consequence of logging and, hence, could have an impact on ape abundance and distribution. It is important to note that the test predictors varied per segment over the course of the study since we

Table 1
Definitions of the predictor variables used and their classification as either “test” (T) or “control” (C) predictors. * = square root transformed to achieve more symmetrical distributions and to avoid influential cases. Tree contagion was also square root transformed after scaling it to a minimum of zero; ˆ = log transformed. All distances were expressed in kilometers. We planned to include Distance to Settlement in the study, but it was correlated with Distance to Park Border and so was removed from the predictors.

Category	Predictor variables (code)	Class	Definition
Human impacts	**Logging History** (bef.dur.aft)	T	Whether survey of segment took place before, during, or after logging.
	Distance to Route* (sqrt.dist.to.routes)	T	Distance between segment midpoint and closest layon or skidder trail.
	Distance to Logging (distance.to.logging.filled)	T	Distance between segment midpoint and nearest ongoing logging. We placed a 10 m × 10 m grid over the logged area and used average distance between midpoints per grid cell and center points of segments as the distance between the segments and the logging activity. For years in which no logging took place, we set the distance to 25 km, a value slightly larger than the largest actual distance between logging activity and a segment center point (22.6 km).
	Weighted Human Impact* (sqrt.weighted.human.impact.per.km)	T	Number of indicators of human activity per segment multiplied by category's weight and then summed as an overall measure of human activity.
Ape resources	**Total Feeding Trees*** (sqrt.tot.feed.tree.value.abs.per.km)	T	Number of trees per species within 150 m from segment, multiplied by the tree species' value as a food source and then summed. Determined separately for chimpanzees and gorillas.
	Total Nest Trees* (sqrt.tot.nest.tree.value.per.km)	T	Number of trees per species within 75 m from segment, multiplied by the tree species' value as a nesting tree and then summed. Determined separately for chimpanzees and gorillas.
Vegetation	**Tree Biomass** (tree.biomass)		Average biomass (DBH) of trees within 150 m from segment.
	Tree Biomass Variationˆ (log.tree.biomass.cv)	T	Proxy for diversity in forest structure with regard to tree size. Calculated as the standard deviation of the biomass, divided by the mean of the biomass of the trees within 150 m of each segment.
	Tree Size Heterogeneity (tree.size.biom.heterogeneity)	T	Measure of the spatial structure in tree sizes. Correlation of the size of trees with that of their nearest neighbor of each tree was determined. Determined for trees within 450 m of segment.
	Tree Species Heterogeneity (tree.contagion.1)	T	Measure of forest heterogeneity with regard to the spatial distribution of tree species in the neighborhood of trees of a given species. Calculated as the averaged Shannon's diversity index (standardized to a maximum of 1), based on the relative frequency distribution with which other tree species occurred as the nearest neighbors of trees of a given species. Trees within 450 m of segments were considered.
	Tree Species Clustering* (sqrt.tree.same.neighbor.prob)	T	Measure of clusteredness of tree species, i.e., proportion of trees in vicinity of the segments (150 m on either side) that had a tree of the same species as their nearest neighbor, averaged across all tree species.
	Tree Diversity Index (tree.shannon)	T	Tree diversity. Determined as Shannon's diversity index (standardized to a maximum of 1, Zar, 1999) for trees within 15 m of the segment.
	Distance to River* (sqrt.dist.to.river)	C	Distance between segment midpoint and nearest river; included since rivers provide human access to remote regions and may influence ape distribution.
	Distance to road	C	Distance of segment midpoint to the closest road; included to control for potential impact of traffic and easier access to forest closer to roads.
	Distance to Park Border (dist.to.pa.border)	C	Distance between segment midpoint and the border of Nouabalé-Ndoki National Park; included to control for the possibility that chimpanzee density might be positively related to proximity to park border (as reported in, e.g., Stokes et al., 2010).
Climate	**Predicted Rain** (predicted.rain)	C	Amount of rainfall during the last 100 days prior to the respective survey; included to control for its potential influence on ape nest decay rate. Since accurate rainfall data were available only from September 2006 on, we first modeled seasonality in rainfall and then used rainfall predicted by the model.

determined them separately for each respective year or passage. This was also the case for the ecological variables for which we considered only those trees actually present during a given survey campaign (i.e., not those that had already been removed). Originally, we planned to further include Distance to Settlement (dist2settlement); however, this variable was significantly correlated with dist.to.pa.border and for this reason we decided to drop it from the set of predictors.

To achieve more symmetrical distributions and to avoid undue influence on the analysis results by a small numbers of outliers we square root transformed dist.to.routes, weighted.human.impact.per.km, tot.feed.tree.value.per.km (for both species and all three scores), tot.nest.tree.value.per.km (for both species), tree.same.neighbor.prob, dist.to.river, and dist.to.road, and square root transformed tree.contagion.1 after subtracting its minimum. We log transformed tree.biomass.cv. All distances were expressed in kilometers.

2.7. Statistical analyses

We fitted separate generalized linear models for chimpanzee and gorilla nests, whereby the full models were nest count ∼bef.dur.aft + sqrt.dist.to.routes + distance.to.logging.filled + sqrt.weighted.human.impact.per.km + sqrt.tot.feed.tree.value.per.km + sqrt.tot.nest.tree.value.per.km + tree.shannon + tree.contagion.1 + sqrt.tree.same.neighbor.prob + tree.biomass + log.tree.biomass.cv + tree.size.biom.heterogeneity + sqrt.dist.to.river + sqrt.dist.to.road + dist.to.pa.border + predicted.rain + autocorrelation + offset(log (segmentlength)).

We included an offset term (McCullagh and Nelder, 1996) to

Table 2
Taxon-specific results of the full model for chimpanzee nest encounter rate with feeding trees rated based on expert opinion.

Variable Name[1]	Estimate	SE	Lower*	Upper*	z	*p*	Min**	Max**
Intercept	− 6.036	1.301	8.669	3.380		[2]	–	–
Logging History: During[3]	0.014	0.135	0.246	0.276	0.103	0.918	0.015	0.048
Logging History: After[3]	0.024	0.107	− 0.181	0.229	0.225	0.822	0.005	0.042
Distance to Routes	0.007	0.005	− 0.004	0.017	1.267	0.205	0.006	0.007
Distance to Logging	− 0.001	0.007	− 0.013	0.012	− 0.090	0.928	− 0.001	0.000
Weighted Human Impact	− 0.055	0.022	− 0.098	− 0.012	− 2.549	0.011	− 0.058	− 0.052
Total Feeding Trees	0.136	0.081	− 0.024	0.297	1.682	0.092	0.125	0.150
Total Nest Trees	− 0.013	0.047	− 0.108	0.082	− 0.279	0.781	− 0.020	− 0.008
Tree Diversity Index	− 0.572	1.070	− 2.740	1.583	− 0.534	0.593	− 0.708	− 0.400
Tree Species Heterogeneity	− 1.867	1.927	− 5.742	2.023	− 0.969	0.332	− 2.226	− 1.631
Tree Species Clustering	1.713	0.909	− 0.092	3.550	1.884	0.060	1.451	1.843
Tree Biomass	0.006	0.012	− 0.018	0.030	0.504	0.614	0.004	0.009
Tree Biomass Variation	0.447	0.906	− 1.319	2.242	0.494	0.621	0.260	0.586
Tree Size Heterogeneity	− 0.667	0.736	− 2.154	0.800	− 0.907	0.365	− 0.753	− 0.518
Distance to River	− 0.003	0.004	− 0.011	0.004	− 0.881	0.378	− 0.004	− 0.003
Distance to Road	0.009	0.002	0.005	0.013	4.400	< 0.001	0.008	0.009
Distance to Park Border	− 0.166	0.020	− 0.206	− 0.126	− 8.275	< 0.001	− 0.169	− 0.163
Predicted Rain	0.043	0.027	− 0.010	0.095	1.569	0.117	0.040	0.046
Autocorrelation Term	0.947	0.077	0.796	1.101	12.269	< 0.001	0.933	0.955

*: lower and upper confidence limit; **: minimum and maximum of estimates derived from case wise deletions of transect segments; (1): for test predictors indicated in bold face $p \leq 0.05$, and for those indicated in italicized bold face $0.05 < p \leq 0.10$; (2): not shown because of having a very limited interpretation; (3): dummy coded with 'before' being the reference category; overall, logging history did not reveal significance (likelihood ratio test comparing the full model with one lacking this effect: $\chi^2 = 0.05$, df = 2, $p = 0.974$); the indicated results refer to the comparison with the reference category, namely 'before'.

account for longer transect segments trivially hosting larger numbers of nests. An autocorrelation term was also employed since it seemed likely that nest counts would be spatially autocorrelated beyond what is explained by the predictors in the model (Fürtbauer et al., 2011). We accounted for autocorrelation as follows: first we fitted a model as shown above but without accounting for autocorrelation. From this model we retrieved the residuals and then averaged, separately for each data point, the residuals of all other data points, whereby we weighted their contribution by their distance to the respective data point. The weighting function had a shape of a Gaussian density function with a mean of zero and a standard deviation determined such that the likelihood of the full model with the autocorrelation term included was maximized. We fitted a total of six such models, three for each, chimpanzees and gorillas, with the assessment of the importance of feeding trees based on the three different methods (see above). Since we believed the food tree preference based on expert ranking to be the most reliable we only report the results of these models in the main text (and the results for the other two methods in the appendix).

Since models with a Poisson error structure (McCullagh and Nelder, 1996) appeared to be clearly overdispersed (minimum dispersion parameter across all six models: 4.79; Gelman and Hill, 2007), we decided to use models with negative binomial error distribution (Hilbe, 2011) instead. None of these models was over- or underdispersed (range of dispersion parameters: 0.85 to 1.06). We checked for absence of collinearity by means of Variance Inflation Factors (VIF; Quinn and Keough, 2002; Field, 2005) which indicated that feeding and nesting tree value were to some extent collinear (VIF for feeding and nesting tree value, respectively, gorillas: 5.91 and 7.31 (feeding preference based), 5.01 and 6.64 (feeding frequency based), 3.54 and 6.05 (expert opinion based); chimpanzees: 6.69 and 7.42 (feeding preference based), 6.30 and 7.43 (feeding frequency based), 5.85 and 6.90 (expert opinion based)). Hence, we decided to additionally fit models including only one of the two (but including all other predictors being present in the full model). Among the other predictors collinearity was not an issue (largest VIF = 3.13). We assessed model stability by means of DFBeta-values (Field, 2005) which we added to the model coefficients obtained for the model based on all data (which allowed evaluating the range of estimates across all case-wise deletions). The resulting models showed good stability (see results). As an overall test of the impact of the 12 test predictors (see above) which avoids the risks of multiple testing we compared each full model with a respective null model (Forstmeier and Schielzeth, 2011) comprising only the four control predictors, the intercept, the autocorrelation and the offset term. For this we used a likelihood ratio test (Dobson, 2002).

As an alternative means of inference and a means to assess the relative importance of the different predictors we used Multi-Model Inference (MMI; Burnham and Anderson, 2002). More specifically, we fitted all possible sub-models that can be constructed with the set of 16 predictors, determined the AIC (corrected for small samples) for each of them and then the Akaike weight of each model. We then summed for each predictor the Akaike weights of all models in which it was included as an indicator of its relative importance. Furthermore, we checked whether the null model (intercept, autocorrelation and offset term only) was included in the 95% best model confidence set (Burnham and Anderson, 2002; Mundry, 2011). We included the autocorrelation term that we had obtained for the respective full model in all models.

We fitted the models in R (version 3.2.3; R Core Team, 2015) using the function glm.nb of the R package MASS (Venables and Ripley, 2002), and to determine 95% confidence intervals of model estimates we used the R function confint. For processing spatial data (e.g., reading shapefiles, converting coordinates from WGS to UTM) we used functions provided by the packages shapefiles (Stabler, 2013), splancs (Rowlingson and Diggle, 2015), and rgdal (Bivand et al., 2015). To construct all possible models to be fitted with a set of predictors we used the function permutations of the package gtools (Warnes et al., 2015).

3. Results

3.1. *Chimpanzees*

For chimpanzees the full model was significant as compared to the null model (likelihood ratio test: $\chi^2 = 30.57$, df = 13, $p = 0.004$). More specifically, we found that nest encounter rate decreased with increasing human impact (Table 2 Weighted Human Impact; Figs. 2 and 6). These revealed that the number of nests per segment tended to increase with the total value of feeding trees in its vicinity (estimate + SE = 0.12 + 0.05, z = 2.33, $p = 0.020$; Fig. 3), but was not obviously affected by the total value of nesting trees (0.05 + 0.03,

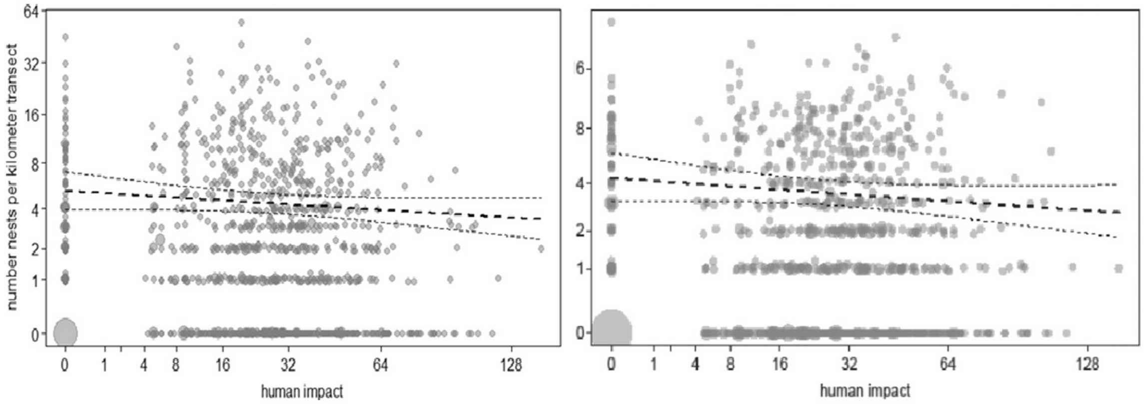

Fig. 2. Influence of human impact on chimpanzee (left) and gorilla (right) nest abundance as indicated by the model with feeding tree value based on expert opinion. The area of the points depicts the number of transect segments with a given number of nests per degree of human impact (range: 1 to 16), the thick dashed line depicts the fitted model and the thin dashed lines its confidence interval.

$z = 1.63$, $p = 0.103$). Summed Akaike weights of the predictors in the chimpanzee model were largest for human impact and two control predictors (Fig. 4, see following section on Control Predictors). The null model was not in the 95% best model confidence set.

The results of the models with tree value based on absolute or relative feeding frequencies were very similar. First, the full null model comparison revealed significance for both models (Appendix Table S3 and S4), and the null model was not included in the respective 95% best model confidence sets of the two models. Furthermore, for human impact both models revealed results virtually identical to those of the model based on expert opinion (Table S3 and S4; Figs. S2 and S3). However, feeding tree value and tree species clustering appeared insignificant in both models. Finally, in the model with feeding tree value based on relative feeding frequency appeared significant (Table S3).

3.2. Gorillas

The full model for the number of gorilla nests tended to differ from the corresponding null model ($\chi^2 = 22.05$, $df = 13$, $p = 0.055$). More specifically, we found that gorilla nest encounter rate was slightly reduced when and where logging took place (overall test of logging history: $\chi^2 = 8.17$, $df = 2$, $p = 0.017$; Fig. 5). Furthermore, gorillas tended to be more common closer to logging zones and in more heterogeneous forest regions (Table 3). Summed Akaike weights were largest for bef.dur.aft, tree.same.neighbor.prob, and also three control predictors (Fig. 4, see following section on Control Predictors). The null model was not in the 95% best model confidence set.

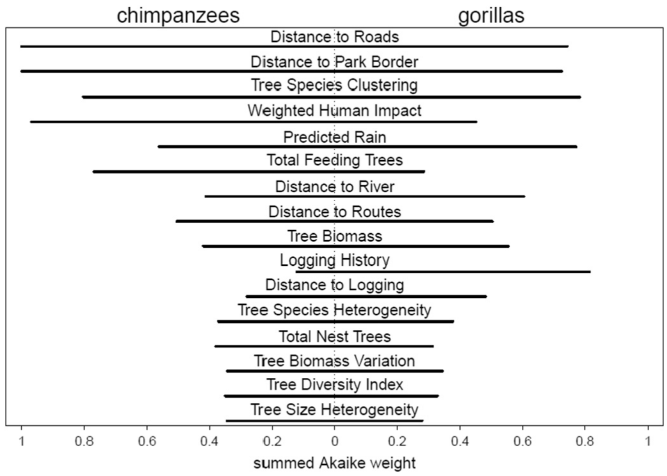

Fig. 4. Akaike weights of the predictors in the chimpanzee and the gorilla model with feeding tree value based on expert opinion. Weights of the intercept and the autocorrelation term are not shown because these were in all models and, hence, trivially one.

The models based on absolute or relative feeding preferences revealed largely the same results. In fact, the full null model comparison revealed significance for both, as did the factor logging history (Tables S5 and S6). As in the model with feeding tree value based on expert opinion, the other two models revealed clear effects for logging history as well as tree.same.neighbor.prob. Multi-Model Inference revealed in case of both models that the null model was not in the 95% best model confidence set. Furthermore, for both models the value of feeding and

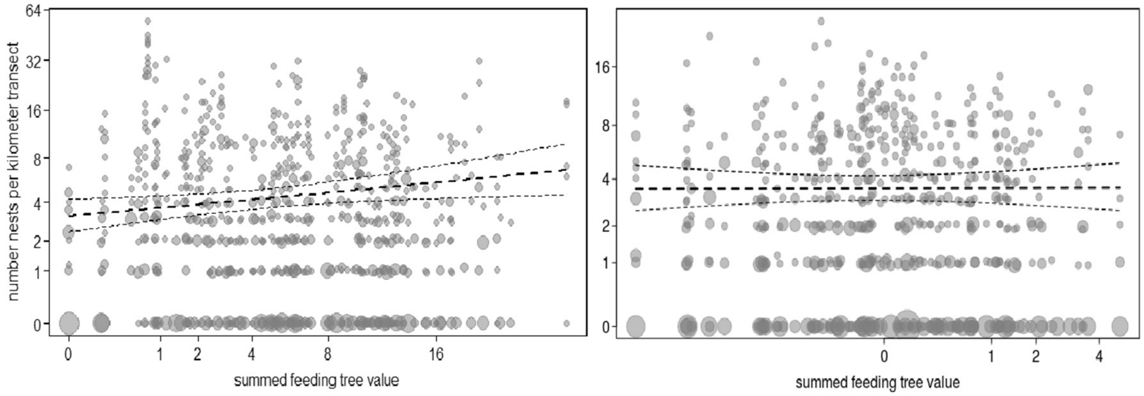

Fig. 3. Influence of total feeding tree value (based on expert opinion) in the vicinity of transect segments on chimpanzee (left) and gorilla (right) nest abundance. The size of the circles depicts the number of transect segments with a given number of nests per degree of human impact (range: 1 to 10), the thick dashed line depicts the fitted model and the thin dashed lines its confidence interval.

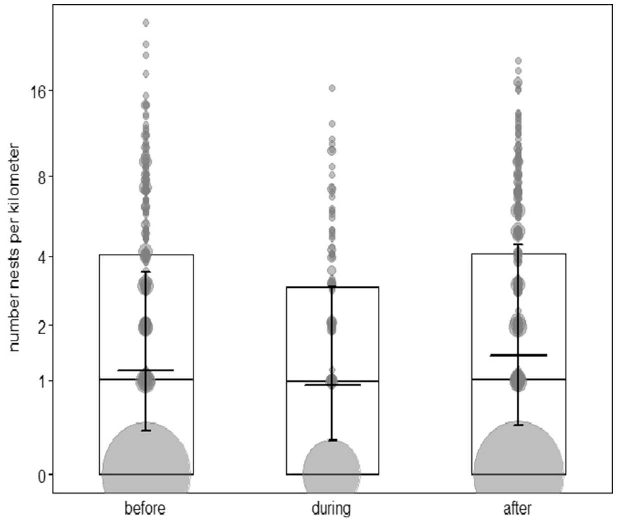

Fig. 5. Influence of logging history on gorilla nest abundance as obtained from the model with feeding tree value based on expert opinion. The area of the points depicts the number of transect segments with a given number of nests per degree of human impact (range: 1–188). Short horizontal lines depict the fitted model whereas long horizontal lines and boxes depict medians and quartiles of the number of nests per transect.

nesting trees, tree species clustering and logging history appeared to be the test predictors with the largest Akaike weights (Figs. 4, S2 and S3).

3.3. Control predictors

Regarding control predictors, the number of chimpanzee nests decreased with increasing distance to the border of the protected area, predicted.rain had a positive impact on gorilla nest encounter rate, and there was clear autocorrelation in all models. We found that the number of chimpanzee nests increased and the number of gorilla nests decreased with increasing distance to roads in the expert opinion model (Tables S3 to S6). The number of gorilla nests tended to increase with increasing distance to the border of the protected area in the expert opinion model. Among the control predictors, Akaike weights were largest for distance to roads and to the border of the protected area for both chimpanzees and gorillas. Rainfall also had a large Akaike weight for gorillas as expected based on seasonal patterns of nest building in western lowland gorillas (Mehlman and Doran, 2002).

4. Discussion

While we found that both chimpanzees and gorillas were adversely affected by logging, we also detected a strong adherence to species-specific ecological profiles and flexible coping strategies which enabled great apes to persist in altered habitats. Chimpanzee responses to human activities occurred at a small, local scale in areas that would be considered within a group's home range. In contrast, gorilla densities varied in response to entire logging fronts which indicated that groups shifted their ranging patterns. We identified microhabitat preferences of sympatric apes by cross-referencing foraging preferences with local timber inventory data, which proved more informative than previous approaches relying on proxies of habitat preference (Poulsen et al., 2011; Stokes et al., 2010). We also examined the potentially cumulative impacts of key contributors such as roads, tree extraction, and forestry camps on local ape populations. In addition to providing empirical support for the ecological needs of endangered African apes, these results convey feedback to forestry managers on the efficacy of reduced impact logging practices and certification schemes on wildlife. We recommend continued monitoring to determine the long-term impacts of logging on great apes and also the impacts of future harvesting cycles in these forests.

Early stages of habitat alteration associated with the first or second logging cycles were hypothesized to be highly disruptive to both chimpanzees and gorillas (Tutin, 2001). However, neither chimpanzee nor gorilla occurrence was dictated by anthropogenic impacts alone. Both species maintained fidelity to their ecological preferences before, during and after logging. Higher numbers of chimpanzee sleeping sites were located in proximity to their preferred fruit trees. In contrast, gorillas were found in more heterogeneous habitats with open canopies which reflected their reliance on non-woody ground vegetation for foraging and nesting. These findings support previous research that forest heterogeneity influences gorilla occurrence at larger scales (Poulsen et al., 2011).

Cumulative impact of logging activity at a given locality was the

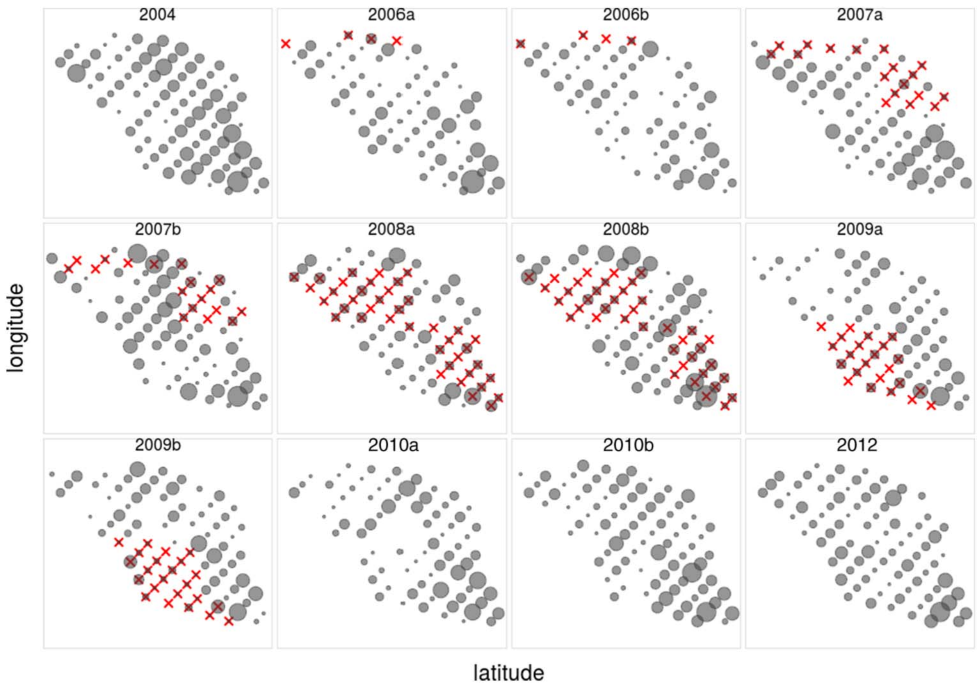

Fig. 6. Spatial distribution of ape nests encountered on transect survey passages conducted from 2004 and 2012 in the Kabo Forestry Management Unit. Size of grey circles indicates relative encounter rate, and red markers indicate presence of human signs associated with logging. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

Table 3
Taxon-specific results of the full model for gorilla nest encounter rate with feeding trees rated based on expert opinion.

Variable Name(1)	Estimate	SE	Lower*	Upper*	z	p	Min**	Max**
Intercept	− 5.990	1.713	− 9.439	− 2.517		(2)	− 6.211	− 5.730
Logging History: During(3)	− 0.218	0.166	− 0.550	0.118	− 1.307	0.191	− 0.239	− 0.196
Logging History: After(3)	0.198	0.133	− 0.070	0.466	1.497	0.134	0.182	0.216
Distance to Routes	0.009	0.006	− 0.003	0.022	1.485	0.138	0.009	0.010
Distance to Logging	− 0.015	0.008	− 0.031	0.001	− 1.912	0.056	− 0.016	− 0.014
Weighted Human Impact	− 0.041	0.026	− 0.093	0.012	− 1.564	0.118	− 0.043	− 0.037
Total Feeding Trees	0.031	0.114	− 0.191	0.255	0.276	0.783	0.013	0.046
Total Nest Trees	− 0.022	0.064	− 0.148	0.103	− 0.350	0.726	− 0.030	− 0.014
Tree Diversity Index	0.657	1.317	− 2.042	3.342	0.499	0.618	0.445	0.863
Tree Species Heterogeneity	− 2.589	2.434	− 7.452	2.293	− 1.064	0.287	− 2.910	− 2.257
Tree Species Clustering	− 2.517	1.121	− 4.614	− 0.406	− 2.245	0.025	− 2.723	− 2.315
Tree Biomass	0.010	0.015	− 0.020	0.040	0.647	0.518	0.008	0.012
Tree Biomass Variation	0.575	1.120	− 1.596	2.784	0.513	0.608	0.344	0.749
Tree Size Heterogeneity	0.363	0.903	− 1.400	2.104	0.402	0.688	0.258	0.535
Distance to River	− 0.008	0.005	− 0.018	0.001	− 1.792	0.073	− 0.009	− 0.008
Distance to Road	− 0.005	0.002	− 0.010	0.000	− 1.954	0.051	− 0.005	− 0.004
Distance to Park Border	0.041	0.024	− 0.007	0.088	1.701	0.089	0.038	0.043
Predicted Rain	0.082	0.032	0.016	0.147	2.516	0.012	0.078	0.084
Autocorrelation Term	0.949	0.183	0.585	1.314	5.171	< 0.001	0.925	0.965

*: lower and upper confidence limit; **: minimum and maximum of estimates derived from case wise deletions of transect segments; (1): for test predictors indicated in bold face $p \leq 0.05$, and for those indicated in italicized bold face $0.05 < p \leq 0.10$); (2): not shown because of having a very limited interpretation; (3): dummy coded with 'before' being the reference category; overall, bef.dur.after appeared significant (likelihood ratio test comparing the full model with one lacking this effect: $\chi^2 = 8.17$, df = 2, $p = 0.017$); the indicated results refer to the comparison with the reference category, namely 'before'.

most influential anthropogenic factor on chimpanzee occurrence. Gorillas avoided areas with active timber extraction, but re-colonized locales immediately after periods of active exploitation. This was reflected in the influence of a particular area's logging history on gorilla abundance, and the temporary use of neighboring refugia by gorillas to avoid areas being intensively harvested. Such an avoidance strategy is only feasible for species that can tolerate spatial overlap between groups and in areas where food resources can support a sudden influx of apes. The immediate decreases in gorilla encounter rates associated with active logging corroborated findings from shorter term studies conducted elsewhere in the region (Arnhem et al., 2008; Haurez et al., 2016; Matthews and Matthews, 2004). Depending upon the intensity and pace of logging, a chimpanzee community or gorilla group may experience several consecutive years of timber extraction within or adjacent to their home range. Understanding the lasting impacts of logging on ape distribution will require further research focused on edge-effects, spatial configuration of access networks such as principle logging roads, and forest regeneration dynamics. Our results confirm previous findings from landscape scale studies that roads and other linear features adversely affected chimpanzees (Stokes et al., 2010). Nest encounter rates of chimpanzees in particular areas remained low for a year or more after logging indicating avoidance. The total clearance of trees on transport corridors reduces habitat, but in cases where roads are abandoned revegetation occurs over years (Kleinschroth et al., 2015). Given the relatively short duration of our study (< 10 years), any long-term inference about the impact of roads and logging on these species is unwarranted at this time and will require a study spanning several decades.

Our findings raise the question of whether these selectively logged forests are transitioning to an environment more suitable for generalist species and what such changes mean for this ape guild. The cumulative effects of repeated harvesting cycles at 30 year intervals in this region remain unknown. Reduction of canopy coverage is likely to be of greater concern for the survival of specialist species whose existence is reliant upon more closed canopy habitats than generalist species. Higher densities of non-arboreal flora such as terrestrial herbaceous vegetation in logged forests compared to neighboring intact forests support assumptions about ongoing post-exploitation succession dynamics (GTAP unpublished data). Brncic et al. (2009) predicted an ongoing transition from more closed canopy to more open forest in this region based on palaeoecological evidence coupled with anthropogenic impacts and predicted climatic changes. Changes in forest structure and tree community dynamics merit further research as they play a vital role in ape survival.

4.1. *Management recommendations and future directions*

Preservation of canopy coverage is a central value of global climate strategies (UNFCC, 2008), establishing forest status (Sasaki and Putz, 2009) and timber certification standards in central Africa (FSC-STD-RoC, 2016), but sustaining forest coverage alone does not ensure the preservation of forest dwelling species (Barlow et al., 2016). As part of certification, the forestry company worked with conservationists and third party auditors to assess and apply adaptive management procedures to safeguard identified environmental values. Regular meetings between the stakeholders to discuss areas of concern and results were productive. Some initiatives provided immediate benefits, such as the deployment of mobile eco-guard units to reduce poaching (Tranquilli et al., 2014). As part of certification, the logging company supported such initiatives. Our post-logging surveys confirmed that once logging was completed, roads and layons were closed and human encounter rate returned to baseline (Morgan et al., 2013). We recommend continued monitoring of this region bordering the NNNP as the potential for increases in hunting pressure is possible considering infrastructure improvements and human population increases (Poulsen et al., 2011).

Forest stand management at the phase of AAC should be an important criterion in assessing the impacts of logging, as it is a well-defined unit that experiences coordinated temporal disturbance and associated landscape modifications (such as road building and timber extraction). For example, minimizing the impacts of logging on apes involves ensuring that tree stems removed are temporally and spatially staggered so as to not encompass the entire home range of gorillas (approximately 7 km^2) or chimpanzees (minimum of 10 km^2) in an AAC area. It was also at the AAC level that we found tree resources important to sympatric ape distribution could be identified from commercial timber inventories. Importantly, few preferred ape food and nesting resources were removed during this second logging cycle due to the company's selectivity of timber and low stem extraction rate. Removal intensity was estimated at < 2.5 trees/ha (Congolaise Industrielle des Bois, 2006) affecting 10 to 20% of the forest canopy which is on the lower end of the disturbance continuum for tropical forestry out takes and disturbance (Putz et al., 2000). However, it is likely that with future off-takes an increasing number of ape resources will either be harvested or compromised by secondary impacts. The demand for timber will continue and diversification of marketable timber is projected given the low recruitment of currently selected timber species in this region (Hall et al., 2003).

Addressing species-specific concerns in accordance with the High Conservation Value (HCV) concept has facilitated more informative and cost-effective forest management. All forestry companies working in the region are required to collect tree inventory data, and so we recommend such an approach be integrated into management plans and regional certification standards. Conservation-oriented tools such as REDD initiatives and Intact Forest Landscapes could also benefit from this approach. Considering that considerable numbers of chimpanzees and western gorillas inhabit industrial logging concessions in this region (IUCN, 2014), the potential benefits of addressing the impacts of logging on ape survival and forest management could be far reaching.

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Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.biocon.2017.10.026.

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