MODELING BONOBO (*PAN PANISCUS*) OCCURRENCE IN RELATION TO BUSHMEAT HUNTING, SLASH-AND-BURN AGRICULTURE, AND TIMBER HARVEST: HARMONIZING BONOBO CONSERVATION WITH SUSTAINABLE DEVELOPMENT

by

JENA RENEE HICKEY

(Under the Direction of NATHAN P. NIBBELINK and JOHN P. CARROLL)

ABSTRACT

Bushmeat hunting is anticipated to directly influence the distribution of bonobos through mortality of individuals and/or indirectly via bonobo avoidance of areas with higher hunting activity. Fragmentation of lowland rainforest is expected to facilitate hunter access to potential bonobo habitat, thereby reducing bonobo occurrence and reducing the effective habitat afforded by fragmented forests. We calculated four bonobo-specific fragmentation metrics based on remotely sensed data and fit univariate logistic regression models relating each metric to bonobo nest occurrence data collected in 2009. We found strong correlation between all fragmentation metrics and bonobo nest occurrence, with nests less likely to occur as fragmentation increased. We ranked the metrics based on predictive accuracy, with forest edge density (ED) ranking the highest. Using a maximum entropy modeling approach and 10 years of collaboratively compiled bonobo nest data, we built the first spatially explicit multivariate model predicting the rangewide distribution of bonobos. Of the rangewide environmental variables tested, the most important were distance from agriculture, distance from roads, ED, percent forest, and distance from river. Except percent forest, we view these predictors as proxies of hunting impact. Areas closer to agriculture are closer to human populations who tend to hunt in the surrounding forest. Roads and

navigable rivers provide human access to areas that would otherwise likely be less vulnerable to hunting. ED distills the information of forest fragmentation from agriculture, logging, major rivers, and roads into a single metric that relates to hunter accessibility. At a finer scale, we fit bonobo site-occupancy models using three landscape-level metrics and three field-derived measures of human activity (machete cuts, traps, and roads). We used an information-theoretic approach to select the best fit models out of 65 potential combinations. ED occurred in all 13 of the top models, machete cuts occurred in 11, and both were negatively correlated with bonobo occupancy. Very likely, it is the poaching associated with these metrics that is the single common threat influencing bonobo occurrence. Our results indicate that forest fragmentation and hunting both negatively influence bonobo occupancy and both landscape- and local-level variables are important considerations in order to conserve this species.

INDEX WORDS: Bonobo, Great ape, Pan paniscus, Fragmentation, Landscape metrics, Bushmeat, Hunting, Landscape planning, Conservation, Landscape ecology, Maringa-Lopori-Wamba, Democratic Republic of Congo

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DEDICATION

With love to my wonderful mother, Barbara, who provided unfailing support to follow my dream, especially when it meant channeling her apprehension into positive thoughts sent around the world.

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CHAPTER 1

INTRODUCTION AND LITERATURE REVIEW

Conservation of biodiversity and specific species of concern necessitates deliberate and informed land-use decisions rather than unmitigated spread of human use. With the global human footprint ever intensifying (Sanderson *et al.,* 2002), natural-resource decision making must proceed even when species-specific biological information is incomplete. To conserve species of interest, natural resource planners rely on a clear understanding of where those species occur and how they react to various human impacts. In an age of rapid land-cover conversion, traditional approximations of species' ranges based exclusively on historic data are insufficient for conservation planning aimed at reducing the impact of infrastructure and pervasive human use. For that reason and in conjunction with the proliferation of available data from remote sensing, the use of satellite imagery to estimate species' distributions has become widespread. Yet, to be truly useful for species conservation, it is important to quantify the accuracy of such data for predicting species occurrence.

Remote areas present a particular challenge for understanding species-habitat relationships because biological data are scarce and difficult to obtain due to inaccessibility. In many cases, even remotely-sensed data, such as satellite imagery, are not easily ground-truthed. Therefore, to make the most of limited spatial and biological data, spatially-explicit rangewide models that deliver fine-scaled information on species occurrence and relative habitat suitability – even in areas that are not surveyed – are critical. Landscape-level variables derived from remote sensing can contribute to models of species' potential habitat and therefore to more informed decisions,

only if they are grounded in established relationships with the elements of biodiversity targeted for conservation. Such models can inform land-use plans designed to maintain connected, viable populations of species.

The bonobo (*Pan paniscus*), epitomizes the remote-area challenge (Nishida 1972). Bonobos occur naturally at low densities in the rainforests of the Democratic Republic of Congo (DRC) and are difficult to locate (Badrian *et al.* 1981, Kano 1984, Mohneke and Fruth 2008). Surveys of unhabituated bonobos tend to focus on the daily nest structures they build, because in areas where they are hunted, bonobos tend to avoid humans (Kano 1984, Van Krunkelsven 2001, Reinartz *et al.* 2006, Fruth *et al.* 2008, Mohneke and Fruth 2008, Reinartz *et al.* 2008, Hart *et al.* 2008, but see Grossmann *et al.* 2008). Persistent civil strife, limited road infrastructure, and food insecurity contribute to the low accessibility of the bonobo range to scientists (Dupain and Van Elsacker 2001, Eba'a Atyi and Bayol 2008, Grossmann *et al.* 2008). The highly rural human population within the bonobo range generally sustains itself through unregulated expansion of slash-and-burn agriculture, bushmeat hunting, and forest-product use (e.g. firewood collection) (Oates 1994, Eba'a Atyi and Bayol 2008, USAID 2010). These extractive activities impact wildlife and fragment Congolese rainforests, home to the only wild populations of bonobos in the world (Fruth *et al.* 2008, USAID 2010).

Given that Congolese communities must hunt, farm, and log to shape their livelihoods, the over-arching goal of this project was to provide information to aid in the development of best management practices for natural resource managers interested in bonobo persistence. To achieve this goal, we aimed to develop landscape-scale metrics that reasonably predict where bonobos occur, to create maps identifying areas with the highest potential to support bonobos, and to

assess the accuracy of such broad-scale metrics against known bonobo occurrences and field-based measures of potential threats.

Our first objective was to identify useful landscape metrics for predicting bonobo occurrence (Chapter 2). To address this objective, we considered aspects of bonobo habitat expected to be both important to bonobos and detectible by satellite imagery. Timber harvest and slash-and-burn agriculture remove trees and forest cover that bonobos use as nesting, foraging, and shelter habitat (Badrian *et al.* 1981, Kano 1984, Kano and Mulavwa 1984, Oates 1994). Furthermore, timber inventories (conducted on cut transects), road networks, logging operations, and small farms penetrate the dense forest with linear openings that facilitate hunter access to bonobos (Wilkie *et al.* 1992, Oates 1994, Dupain *et al.* 2000, Dupain and Van Elsacker 2001). It is possible then that logging and farming not only reduce bonobo habitat through tree removal, but these activities may actually lead to increased harvest rates of bonobos. Although not a primary species for subsistence consumption, bonobos are eaten and can be sold for considerable profit in urban markets or as part of the pet trade (Dupain *et al.* 2000, Dupain and Van Elsacker 2001). While satellite imagery cannot detect hunting explicitly, remote sensing can capture the forest fragmentation that exacerbates hunting and pet trade activities. In fact, habitat fragmentation and hunting are now considered principal threats to primates in general (Arroyo-Rodriguez and Mandujano 2008), and have been regarded as such for bonobos specifically for at least 25 years (Kano 1984). Therefore we sought to distill the information of forest fragmentation into one or more metrics and test them.

We calculated four broad-scale landscape metrics for predicting bonobo occurrence: edge density (ED), COHESION, CONTAGION, and class area (CA) for the Maringa-Lopori-Wamba (MLW) landscape and evaluated them for utility in predicting bonobo-nest occupancy based on

2009 field data. We conducted extensive field surveys entailing over 1,000 km of river and motorbike travel to then access different regions on foot. We fit logistic regression curves for bonobo nest occurrence for each metric and cross-validated them with hold-out data to independently test their accuracy. In this manner, we hoped to suggest an appropriate metric to use in future multivariate models of bonobo distributions.

Our second objective was to develop the first spatially explicit model of the rangewide bonobo distribution. Such a model would provide conservation planners a map of areas likely to support bonobos and that may be good candidates for protected area expansion, as well as the complimentary information regarding areas less suited to sustaining bonobos where expansion of human uses may do the least-harm (Chapter 3). We used a machine-learning approach to species distribution modeling called maximum entropy (MaxEnt; Phillips *et al.* 2006; Elith *et al.* 2010), in which attribute data associated with known locations of bonobo nests were used to predict locations of suitable conditions across the species' entire range. Numerous research teams collected bonobo nest data throughout the bonobo range between years 2000 and 2010 and we compiled these data for use in this modeling effort. Starting with numerous landscape-scale environmental predictor variables, including forest fragmentation, we systematically tested their relative capacity to predict bonobo nest blocks in multivariate MaxEnt (version 3.3.1) models. We excluded variables that contributed negligibly to prediction and interpreted the potential mechanisms relating the landscape-scale predictors to bonobo nest presence.

Finally, in Chapter 4, we evaluated the relative influence of landscape and local variables related to human presence and hunting on the occupancy of bonobos. We fit multiple alternative models for predicting bonobo occupancy, including all combinations of broad-scale remotely-derived data and fine-scale field-derived data. In addition to the fragmentation metric from

Chapter 2, we calculated two additional landscape-level metrics thought to correspond to human access and potential hunting pressure: distance from fire and distance from river. To compliment these remotely derived predictors with field data, we recorded bonobo nests and evidence of potential human threats within the MLW in areas of different hunting pressure. Such evidence included: machete cuts in vegetation, traps, hunting camps, paths, roads, and log-cut trees. We used an information-theoretic approach to select the best fit models, model averaged the parameter estimates, and evaluated the direction, magnitude, and confidence interval for each predictor. By grounding remotely-sensed predictors with field-based evidence of bonobo occupancy and relative hunting pressure, we sought to elucidate the mechanisms by which landscape-level variables influence bonobo distributions. Equipped with information regarding the relationships between bonobo occupancy and various human activities, we hope that conservation planners can encourage proactive management of land uses. Timber harvest units, agricultural fields, protected areas, and hunting areas can be placed strategically in an effort to meet local communities' needs while doing the least harm to bonobo populations.

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CHAPTER 2

APPLYING LANDSCAPE METRICS TO CHARACTERIZE POTENTIAL HABITAT OF BONOBOS (*PAN PANISCUS*) IN THE MARINGA-LOPORI-WAMBA LANDSCAPE, DEMOCRATIC REPUBLIC OF CONGO[1]

[1] [1]Hickey, J.R., J.P. Carroll and N.P. Nibbelink. 2012. *International Journal of Primatology*. 33:381-400. Reprinted here with permission of the publisher.

ABSTRACT

To conserve areas and species threatened by immediate landscape change requires that we make planning decisions for large areas in the absence of adequate data. Here we study the utility of broad-scale landscape metrics as predictors of species occurrence, especially for remote areas where there is a need to make the most of limited spatial and biological data. Bonobos (*Pan paniscus*) are endangered great apes endemic to lowland forests of the Democratic Republic of Congo. They are threatened by bushmeat hunting that is exacerbated by habitat fragmentation through slash-and-burn agriculture and timber harvest. We developed four landscape metrics: edge density (ED), COHESION, CONTAGION, and class area (CA) that may serve as surrogates for measuring accessibility of areas to hunting in order to predict relative bonobo-habitat suitability. We calculated the metrics for the Maringa-Lopori-Wamba (MLW) landscape and evaluated them for utility in predicting bonobo-nest occupancy based on 2009 field data. Cross-validations showed that all four metrics performed similarly. However, forest edge density (ED) was arguably the best predictor, with an overall classification accuracy of 72.1% in which 85% of known nest blocks (n=124) were classified correctly. We demonstrated that for a relatively intact landscape and a mobile forest-dwelling species that is fairly tolerant of forest openings, forest fragmentation can still be an important predictor of species occurrence. We suggest that ED can be helpful when mapping bonobo habitat in MLW and can aid landscape-planning and conservation efforts. Our approach may be applied to other edge-sensitive species especially where high-resolution data are deficient.

KEYWORDS

bonobo, *Pan paniscus*, edge density, landscape metrics, fragmentation

INTRODUCTION

Remote areas present a challenge for understanding species-habitat relationships because both biological and habitat data are scarce and difficult to obtain. Predicting species distributions generally depends upon having two primary types of data: (1) geographic locations of the species in question and (2) variables associated with those locations and the entire area of interest, such as vegetation cover type, soil type, or elevation (Austin 1996). Statistical relationships are investigated to determine the likelihood of species occurrence given a range of environmental conditions (Franklin 1995, Austin 1998, Guisan and Zimmermann 2000, Ferrier *et al.* 2002, Elith *et al.* 2006). Species location data can be scarce in remote areas due to inaccessibility and this inaccessibility also complicates the collection of observations to ground-truth the classification of remotely-sensed data that may exist, such as satellite imagery. Yet for endangered species, conservation planning must proceed in these data limited scenarios and such planning relies on reasonable estimates of species distributions.

The bonobo (*Pan paniscus*) epitomizes the remote-area challenge (Nishida 1972). Bonobos occur naturally at low densities and are difficult to locate (Badrian *et al.* 1981, Kano 1984, Mohneke and Fruth 2008) in the rainforests of the Democratic Republic of Congo (DRC). Although decades of effort have been invested in wild bonobo studies (Susman 1984, White 1996, Furuichi and Thompson 2008), much of that work has been on habituated populations (Furuichi 1987, Kano 1992, Furuichi *et al.* 1998, Furuichi and Thompson 2008, Hohmann and Fruth 2008). Surveys of unhabituated bonobos tend to focus on the daily nest structures they build, because in areas where they are hunted, bonobos tend to avoid humans (Kano 1984, Van Krunkelsven 2001, Reinartz *et al.* 2006, Fruth *et al.* 2008, Mohneke and Fruth 2008, Reinartz *et al.* 2008, Hart *et al.* 2008, but see Grossmann *et al.* 2008). Persistent civil strife, limited road

infrastructure, and food insecurity contribute to the low accessibility of the bonobo range to scientists (Dupain and Van Elsacker 2001, Eba'a Atyi and Bayol 2008, Grossmann *et al.* 2008). The highly rural human population within the bonobo range generally sustains itself through unregulated expansion of slash-and-burn agriculture, bushmeat hunting, and forest-product use (e.g. firewood collection) (Oates 1994, Eba'a Atyi and Bayol 2008, USAID 2010). These extractive activities impact wildlife and fragment Congolese rainforests, home to the only wild populations of bonobos in the world (Fruth *et al.* 2008, USAID 2010). Determining effects of these activities on bonobo distributions can guide future research and aid landscape planning efforts.

Ongoing conservation efforts are grappling to determine priority areas for research, monitoring, and protected-area designation for bonobos (Luetzelschwab 2007). To address the urgent call for landscape planning in the face of the above data limitations, there is a need to identify broad-scale landscape variables, derived from remotely-sensed data, and test their ability to identify high quality bonobo habitat. While increased data collection would be ideal, we were interested in exploring the utility of broad-scale landscape metrics to bridge the gap, thereby providing a near-term solution until more species-location and high-resolution data become available. To develop a bonobo-relevant metric, we considered aspects of bonobo habitat expected to be both important to bonobos and detectible by satellite imagery. Timber harvest and slash-and-burn agriculture remove trees and forest cover that bonobos use as nesting, foraging, and shelter habitat (Badrian *et al.* 1981, Kano 1984, Kano and Mulavwa 1984, Oates 1994). Furthermore, timber inventories (conducted on cut transects), road networks, logging operations, and small farms penetrate the dense forest with linear openings that facilitate hunter access to bonobos (Wilkie *et al.* 1992, Oates 1994, Dupain *et al.* 2000, Dupain and Van Elsacker 2001). It

is possible then that logging and farming not only reduce bonobo habitat through tree removal, but these activities may actually lead to increased harvest rates of bonobos. Although not a primary species for subsistence consumption, bonobos are eaten and can be sold for considerable profit in urban markets or as part of the pet trade (Dupain *et al.* 2000, Dupain and Van Elsacker 2001). While satellite imagery cannot detect hunting explicitly, remote sensing can capture the forest fragmentation that exacerbates hunting and pet trade activities. In fact, habitat fragmentation and hunting are now considered principal threats to primates in general (Arroyo-Rodriguez and Mandujano 2009), and have been regarded as such for bonobos specifically for at least 25 years (Kano 1984). Therefore a metric that captures this fragmentation may be a useful predictor of bonobo occurrence.

This study focuses on the process of creating 4 bonobo-specific fragmentation metrics from available Landsat Thematic Mapper (TM) products. In order to determine the utility of these metrics to identify potential habitat for bonobos in the face of limited available high-resolution spatial data, we evaluated their ability to predict bonobo nest occurrence in MLW and discuss their potential value for broad scale habitat-suitability modeling and management applications.

There are many potential metrics one could use to estimate habitat fragmentation. Selection of a fragmentation metric is challenging because quantifications of fragmentation and habitat loss have been shown to be confounded (Fahrig 2003, Neel *et al.* 2004) in that fragmentation itself is caused by dispersed habitat loss, resulting in a correlation between the two measures. Neel *et al.* (2004) examined numerous metrics across gradients of aggregation and percent habitat (area). Aggregation is a measure of the degree to which pixels of a focal class (say, forest) are spatially clustered. Conceptually, aggregation is similar to connectivity and is essentially the inverse of fragmentation. Neel *et al.* (2004) showed that certain landscape metrics

purported to measure aggregation are sometimes more highly correlated with percent habitat (*P*) than with aggregation. This non-intuitive behavior adds to the difficulty in selecting appropriate metrics.

We evaluated: forest edge density (or, ED, the linear edge between forest and non-forest in a given area), COHESION, CONTAGION, and class area (CA) of forest, as predictors of bonobo occurrence (Table 2.1). We expected ED (McGarigal and Marks 1995) to be useful as a broad landscape metric that simultaneously captures the importance of intact forest (low ED) and the concomitant negative impacts of forest loss and forest fragmentation (high ED). A strength of the conceptually intuitive ED metric is that it has a strong negative correlation (Kendall's τ=-0.79) with aggregation (Neel *et al.* 2004) which translates to a positive correlation with fragmentation. However, there is no perfect metric. The weakness of ED is that it exhibits a parabolic response in relation to percent-habitat, *P*, hypothetically represented in Figure 2.1. This means that as area of target habitat nears 50% of the landscape, the potential for high ED will be highest (Li *et al.* 1993) (e.g. complete disaggregation of forest pixels is possible, as in a checkerboard). While this parabolic behavior may at first seem problematic, because there is the potential for similar ED values at different levels of forest disturbance, it is still true that complexity of patch edge influences ED such that for the same *P*, convoluted edges result in higher ED than simple edges (Hargis *et al.* 1998, Fahrig 2003). Therefore, ED can highlight differences in edge within a narrow range of *P* values. For landscapes with a wide range of *P* values, one could multiply ED by CA of forest such that the interaction term would capture the entire 0-100% range. Either of these approaches is likely to capture useful information on landscape pattern for species responding to edge effects (Donovan *et al.* 1997, Chalfoun *et al.* 2002). In our highly forested study area, we expected *P* values predominantly in the upper tail of the ED-*P* curve (Figure 2.1)

and for bonobo occurrence to decline with increasing ED; therefore for simplicity we used ED alone.

We chose COHESION because it proved to be a useful predictor of dispersal for another highly-mobile forest-associated species, the northern spotted owl (*Strix occidentalis caurina,* Schumaker 1996, UMass 2000). However, COHESION is non-intuitive because, although it was originally conceived as a measure of aggregation or connectedness, it was later found to correlate more strongly with quantity of habitat (τ=0.88) rather than aggregation (τ=0.12) (Neel *et al.* 2004).

We chose CONTAGION (Li and Reynolds 1993) because it was originally created to capture both the degree to which habitat patch types are mixed and the spatial distribution of patch types at the landscape level (McGarigal and Marks 1995). However, CONTAGION's ability to represent spatial distribution of habitat patches is disputed (Hargis *et al.* 1998). Generally, lower CONTAGION indicates a more mixed pattern of different patch types and higher CONTAGION indicates more aggregation of like patch types in a landscape. We expected a positive correlation between bonobo occupancy and both COHESION and CONTAGION.

We chose CA in order to compare fragmentation metrics to simple habitat loss and to evaluate where our study landscape, Maringa-Lopori-Wamba (MLW), resides on the *P* gradient.

METHODS

Study Area

The study area, MLW, is an area designated as a conservation landscape by the Central African Regional Program for the Environment (CARPE), a branch of the U.S. Agency for International Development (USAID) (Hickey and Sidle 2006). MLW (Figure 2) was selected as a CARPE landscape specifically for the conservation of bonobos in conjunction with alleviation of poverty

(Hickey and Sidle 2006). MLW is approximately 74,000 km^2 and characterized by large areas of intact lowland rainforest, human settlement, slash-and-burn agriculture, and numerous large timber concessions (totaling >6,000 km^2) in different states of harvest rotation or harvest planning (Dupain *et al.* 2009).

Focal Area Selection

In order to determine the range of fragmentation values in MLW (of four landscape metrics with values for each pixel based on a 20-km^2 window around each pixel; see *Calculating Landscape Metrics*) in relation to land use, we selected 3 focal areas (Figure 2). Each focal area was approximately 430 km^2 in size and represented one of the 3 most typical land use categories: minimum use, logging use, and human-settlements, respectively. The minimum-use area was selected based on continuous high canopy cover, absence of roads, and distance from detectable human activity. We assumed this minimum-use area represents optimal bonobo habitat and likely provides a bookend-reference point for greatest habitat quantity/quality based on least fragmentation achievable in MLW. The logging-use area was selected for its regular grid-like pattern of logging-access roads in an area with no detectable human settlements. We assumed the logging-use area represents an area in which bonobo-habitat value is reduced by the level of fragmentation. Such fragmentation may allow increased hunter access and, subsequently, either increased harvest of bonobos or avoidance of the area by bonobos. The human-settlement area was selected for the known high human population, large interruptions in forest canopy due to the presence of villages and agriculture, and the absence of nearby logging. This human-settlement area represents the opposite end of the spectrum from the minimum-use area and provides a reference for maximal levels of fragmentation within MLW as of 2000.

Development of base forest-cover layers

We used 7 scenes of Landsat TM imagery circa 2000 as classified for the USAID-CARPE decadal forest change mapping project with a pixel size of 57x57 m (Hansen *et al.* 2008). The original classification portrayed each pixel as the likelihood (from 1 to 99%) of having at least 60% canopy cover (henceforth termed "forest"). Hansen *et al*. (2008) validated the classification using MODIS (MODerate Resolution Imaging Spectroradiometer) data, with a coarser resolution of 231 m which is atypical of most validation processes. Ideally, finer grained imagery or field reconnaissance would inform the validation process; but again, this remote area was deficient in data, including high resolution data. Although more recent imagery (circa 2010) has since been classified in a similar manner, it was not available at the time of these analyses. We expect the 9-year difference between satellite images and field data is negligible for these analyses because the amount of forest loss between 2000 and 2010 was <0.44% of MLW (OSFAC 2010).

In order to calculate landscape metrics, we first had to establish binary habitat types from the original classification. Using ESRI's ArcMap version 9.3 we reclassified the probability of being forested into a binary raster (FOR) where 0 = unforested (0-30% likelihood of being forest) and 1 = forested (31-99% likelihood of being forest). Likelihood of forest cover was allowed to range widely (31-99%) for the definition of forested habitat because bonobos are tolerant of low canopy cover and openings (Uehara 1990, Thompson 1997) in the absence of human activity (i.e. hunting) and have been documented in some forest-savannah mosaics (Inogwabini *et al.*2008). In addition, several different thresholds were compared to Google® Earth imagery in the few locations where high resolution data was clearly visible, and the 30% threshold appeared to best capture forest/non-forest habitats. Because we had access to reasonably good spatial data for roads and rivers (CARPE-UMD 1997, Lehner *et al.* 2006) which are not always classified as

nonforest in many areas of the Landsat-derived data, we created two additional forest/nonforest layers on which to base landscape metrics in order to test the value of this additional information. Due to documented reduced bonobo numbers around roads (Dupain and Van Elsacker 2001, Dupain *et al.* 2000, and Horn 1980), we buffered roads 100 m on either side and added the buffered roads to the unforested class, to create a second base layer (referred to as RD). Finally, because of increased access and hunting activity near rivers, we buffered both roads and rivers by 100 m and added those buffered areas to the unforested class, for a third base layer (referred to as RR, for roads and rivers).

Calculating Landscape Metrics

Because we were interested in comparing the ability of 4 landscape metrics to predict bonobo presence across all of MLW, including sites we never surveyed, we needed to build spatially explicit raster layers of each metric across the entire landscape. We conducted a moving window analysis in FRAGSTATS Version 3.3 (McGarigal *et al.* 2002) to calculate ED, COHESION, CONTAGION, and CA on each of the above 3 base forest-cover layers (FOR, RD, and RR). We assumed that home-range size is the scale at which bonobos respond to fragmentation, and therefore applied a radius of 2.524 km to the moving windows to approximate the mean area (20-km^2) of a bonobo-group homerange (Hashimoto *et al.* 1998). The value of each metric within a given window was then assigned to the centroid of that window. By stepping these windows across the entire landscape, this procedure results in a raster with a home-range scaled landscape metric assigned to every pixel. We also ran moving-window analyses on the three focal areas, to investigate the nature of the metrics along a relative continuum of impacted areas. We employed a 4-cell rule for neighborhood size.

ED was reported as a positive number, with larger values indicating greater fragmentation. An ED value of 1 m/ha converted to 1 km of edge/10 km^2 and equated to 2 km of edge across a given 20-km^2 window. COHESION of forest was a positive number <100, with higher values indicating more connected (less fragmented) forest. Similarly, CONTAGION was a positive number ≤100, with larger numbers indicating more aggregation of like patch types. CA of forest was simply the forested area in ha within each moving window and ranged from 0 to 2000 ha. In order to investigate if ED is a potentially useful metric for this landscape, we converted CA to percent-forested habitat, *P*. This allowed us to assess whether MLW represents a relatively narrow portion of the *P* gradient (Neel *et al.* 2004, Hargis *et al.* 1999).

Field Verification

We randomly stratified survey sites *a priori* to represent a range of fragmentation levels, including logged and unlogged areas. Because our premise is that bonobos may avoid highly fragmented areas due to the potential for increased hunting pressure in those areas, we also stratified by protected status, distance-from-fire (a proxy for villages), and distance-from-river (a proxy for human access sites). In this way, we assured that fragmentation was explored across a gradient of potential hunting pressure. In 2009, we conducted line-transect surveys for bonobo nests (Figure 2) using double-independent observer techniques (Williams, Nichols & Conroy 2002). Start and end points of all transects were generated randomly in ArcMap (ESRI, version 9.3) for each strata described. We completed approximately 73 km of line-transect surveys, all of which were surveyed twice, once each by two separate observation teams. We recorded the geographic coordinates of the transect point located perpendicularly to both singly- and doubly-observed nests, as well as other sign (other sign not analyzed here). We complied with protocols

approved by the University of Georgia's Institutional Animal Care and Use Committee (AUP # A2009-10042) and adhered to the legal requirements of the DRC.

Designation of nest blocks and random blocks

Bonobo nests tend to occur in groups and would be expected to be clustered on the landscape (Mulavwa *et al.* 2010). To reduce this spatial auto-correlation, we decreased the resolution of our individual nest locations to 57 x 57 m blocks (the same resolution as our Landsat TM imagery classification; Hansen *et al*. 2008). A block with one or more nest in it was termed a *nest block*. For a comparison set of random (non-nest) blocks that we surveyed with effort equal to nest blocks, we created random points on the transects that fulfilled the criteria of being ≥100 m both from nest blocks and from each other. The 134 random points were distributed proportionally to each transect based on its length compared to the total length of all transects surveyed. It is worth noting that these random blocks do not equate to known absences, because bonobo nests could have occurred there in the past. Since bonobo nests decay between about 75 and 99 days (Mohneke and Fruth 2008), bonobos could have used these random blocks any time in excess of 3 months previous to our surveys.

Logistic Regression Modeling of Bonobo Nest Occurrence

Using logistic regression analysis (Neter *et al*. 1989) in SAS (v. 9.1), we examined the individual relationships between nest-block occurrence and ED, COHESION, CONTAGION, and CA. We input 124 nest blocks (1), 134 random blocks (0), and their corresponding landscape-metric value into logistic regression models (one model for each landscape metric, separately). To test for multicollinearity, Pearson's correlations (r) were calculated between all pairs of variables to assess if multiple landscape metrics could be included in a multivariate model. We ranked the metrics based on their leave-one-out predictive error rates to select one for mapping (Kearns *et al.* 1997,

Kearns and Ron 1999). In logistic regression the coefficients are expressed in log odds; therefore, in order to calculate an odds ratio, the parameter estimate for the coefficients must be back-transformed with the exponential function, e^x, where x is the logistic parameter estimate. This procedure allows inference of the relationship between the predictor and response variables (Hosmer and Lemeshow 1989). Therefore, we calculated odds ratios for the selected metric in order to infer the direction and magnitude of the relationship with nest-block occurrence. Odds ratios >1 indicate positive relationships, such that with each unit increase in the variable, the probability of occurrence is e^x times greater. Odds ratios <1 indicate a negative relationship and are interpreted more easily by taking the inverse and stating "nest blocks are $1/ e^x$ times" *less* likely to occur with each unit increase in the parameter.

Fragmentation Thresholds

While landscape variables are often useful for habitat modeling in their continuous form, it is often necessary to choose a threshold for visualization and planning. To that end, we produced fragmentation maps based on 3 threshold choices. The Continuous Map (no threshold) simply depicts the continuous gradient of fragmentation values across MLW. Next, because conservation planners may be interested in a distinct demarcation between acceptable and unacceptable amounts of canopy alteration in bonobo habitat, we applied two fragmentation thresholds resulting in binary maps. To assign defensible thresholds, we evaluated fragmentation values using Jenks' natural breaks (Jenks 1967) to identify a natural break in the landscape metric data (Habitat Threshold) and we determined the maximal fragmentation value where bonobo nest blocks were found (Nest Threshold) (see *Results*). The Jenks procedure defined categories by maximizing inter-class variance and minimizing intra-class variance for ED across MLW. The

Habitat Threshold allowed the data on forest pattern to define the threshold, whereas the Nest Threshold allowed the data about bonobo nest occurrence to define the threshold.

RESULTS

Landscape Metrics

All four landscape metrics (Figure 3) were highly correlated with each other (Pearson's $|r| > 0.95$). The strongest correlations were between CONTAGION and CA (r=0.989), followed by CONTAGION and COHESION (r=0.987), and by CONTAGION and ED (r=-0.982) (N=258 for all comparisons). Evaluating all metrics across all 3 base layers, we found ED consistently ranked as the first or second for correlation with bonobo nest occurrence (r=-0.5 for ED-RD), whereas the other metrics frequently ranked 3rd or 4th. Furthermore, leave-one-out cross validations also ranked ED the highest (see *Results - Logistic Regression*). Therefore, we discuss only ED in more detail. ED-RD values ranged from 0 to 104 m/ha across MLW (Figure 3). The mean ED for MLW was 9.83 ± SE 0.003 m/ha. ED was higher (42.6 ± SE 0.06 m/ha) in the human-settlement area compared to all other focal areas (Figure 4). The minimum-use area had virtually no ED (3.06 ± SE 0.015 m/ha), whereas the logging-use area had slightly higher ED as compared to the entire MLW. The mean ED for each focal area was significantly different than that of MLW ($p<0.01$ for all comparisons).

The Jenks (1967) natural breaks procedure demonstrates that there is a natural break around 6.56 m/ha (equivalent to 13.12 km of edge within a 5.048-km diameter home-range) which defines well the difference between minimum-use and logging-use areas (Figure 5). The vast majority of pixels in the minimum-use area had an ED less than 6.56 m/ha, whereas the majority of the logging area had EDs between 6.56 and 18.71 m/ha. Additionally, over 60% of MLW had an ED less than 6 m/ha and over 80% had an ED less than 19 m/ha. Furthermore, we

converted CA to percent habitat, *P*, and found that >90% of MLW was >80% forested, demonstrating that MLW represents a sufficiently narrow portion of the *P* gradient to warrant the use of ED as a measure of fragmentation. As we predicted, most areas were in the upper tail of the ED-*P* curve (Figure 2.1), therefore ED can be expected to be negatively correlated with percent-habitat and positively correlated with forest disturbance in MLW (Neel *et al.* 2004).

Field Verification

During 2009, we completed approximately 73 km of line-transect surveys and recorded the geographic coordinates of 338 bonobo nests. Multiple nests occurring within a single 57-m pixel of our base GIS data layers were treated as a single observation resulting in 124 total nest blocks.

Logistic Regression Modeling of Bonobo Nest Occurrence

Due to the high correlations found among the landscape metrics, they appear to contain nearly the same information and therefore should not be included together in the same predictive model (Neter *et al.* 1989). Hence we were interested in ranking their classification accuracy in order to select a single best predictor. Leave-one-out cross validation performed on single-variable logistic regression models confirmed that ED, COHESION, CONTAGION, and CA predicted bonobo-nest occurrence similarly in all instances. Their predictive error rates, which reflect the sum of the false positive (commission) and false negative (omission) rates, ranged from 27.91 to 30.62%. We ranked all the metrics based first on predictive error (lower is better) and based second on true positive rates (higher is better) (Table 2.2). The top 3 predictors all had a predictive error rate of 27.91% and included ED calculated on FOR, ED calculated on RD, and CONTAGION calculated on FOR. While we acknowledge the merit of CONTAGION as a fragmentation metric, as well as the strong similarity in predictive capability of all the calculated metrics, we selected ED for our maps, due both to its high ranking here and to its ease in interpretation over the other metrics. Note that the model containing CA-RD as a sole predictor had an exceptionally high true positive

rate of 95%; however this model had a substantially higher commission error than the top 3 models (52% versus 40%). Therefore, although the model looks strong initially, its ability to discriminate is marginal in comparison to the top models. While we ran 12 separate logistic models, one for each landscape metric and base forest-cover layer, we summarize the results of the four models run on the intermediate representation of forest cover, the RD base layer (Table 2.3). As mentioned earlier, all metrics performed similarly as predictors of bonobo nest occurrence, and ED ranked consistently the highest. As an example, a confusion matrix (Figure 6) describes the strengths and weaknesses of the logistic ED-RD model in classifying bonobo occurrence.

For proper inference we transformed the log odds parameter estimate (-0.255) in the ED-RD logistic model ($e^{-0.255}$=0.775); and because 0.775 is <1 the odds ratio indicates a negative relationship between ED and nest-block occurrence. Therefore, nest blocks were (1/0.775)=1.3 times *less* likely to occur for each 1-km increase of edge per 10 km^2. Or more simply, about one-third fewer nests were expected to occur, for each unit increase in ED.

Fragmentation Thresholds

Continuous ED and binary-thresholded ED maps were produced for the three focal areas and for all of MLW (Figure 7). The Habitat Threshold map uses a threshold ED of 6.56 m/ha, the natural break in ED values across the landscape and between minimum-use and logging-use areas. The Nest Threshold map uses a threshold ED of 12.256 m/ha, the highest ED value for a nest block from our field verification surveys.

DISCUSSION

Our comparison of prediction accuracy of landscape metrics derived from remotely sensed data demonstrated that fragmentation, no matter how we measured it, is a useful predictor of bonobo nest presence; therefore we encourage the use of a single, well-chosen fragmentation metric for use in multivariate bonobo distribution or habitat-suitability models. The four bonobo-relevant landscape metrics, each classified to represent the potential tolerance of bonobos to open canopy and edge effects, were highly correlated with each other and performed similarly in predicting bonobo nest presence. We favor the use of ED because it ranked highest in leave-one-out cross-validations (Table 2.2) and perhaps, more importantly, because it is the most intuitive representation of fragmentation (Table 2.1). Our field surveys demonstrated that bonobo nest block occurrence was indeed higher where ED (fragmentation) was lower. We found ED, as we calculated it, to be a useful predictor of nest occurrence and potential bonobo nesting habitat. Although ED-RD is merely a single-variable model, it boasted 72.1% overall prediction accuracy and correctly classified 85% of nest blocks.

There is precedent for including ED in evaluations of sustainable management in multi-owner landscapes (Gustafson *et al.* 2007) and as an indicator of conditions for edge-sensitive species (USFS 2004). With that in mind, future land managers may desire a binary ED value either for assigning areas worthy of protection or for assessing acceptable levels of canopy alteration in multiple-use landscapes (e.g. extractive zones or community-use zones, Hickey and Sidle 2006). Ultimately, selecting a threshold for management choices such as allowable canopy alteration is an arbitrary decision, yet to be defensible requires scientific rationale. Therefore, we explored the range of fragmentation (ED) values in relation to land use in MLW. We identified a natural break in MLW-wide ED values that corresponded to the difference between the minimum-

use and logging-use areas. Our field data supported this break as biologically meaningful to bonobos because greater than 92% of nest blocks had an ED<6.56 m/ha, the natural break, and no nests were observed in the logging area. Based on the natural break in ED values for the landscape and the ED values in nest blocks, we offer two thresholds that are supported by the data from MLW. The Habitat Threshold employed the natural break in ED values (6.56 m/ha) to define the threshold, whereas the Nest Threshold allowed the maximal ED (12.256 m/ha) found in a bonobo nest block to define the threshold.

Because conservation spending can depend heavily on visualization of habitat and species ranges (Halpern *et al.* 2006), we advocate careful selection of thresholds both for communicating results and for conservation planning. In order to display potentially acceptable and unacceptable amounts of canopy alteration in bonobo habitat, we produced maps of the Continuous ED metric and two alternate ED thresholds for consideration. The Continuous map allows visualization of how fragmentation changes across the landscape. This depiction can be satisfying in that it is easy to perceive the gradient of fragmentation intensity, differentiating areas that are highly fragmented, from those that are marginal but might be threatened. The continuous metric is also preferred for potential inclusion in bonobo-habitat suitability models, along with other covariates (e.g. landcover, elevation). Eventually, multivariate models will be needed that take several other such explanatory variables into account. All maps portray the range of impact conditions present in MLW circa 2000. Each depicts very low levels of suitably continuous forest for bonobo nesting in the human-settlement area, which is supported by field reconnaissance near the village of Djolu (Hickey and Sidle 2006) and previous research (Kano 1984). Furthermore, all maps portray suitably contiguous forest in the minimum-use area which we interpret as a reasonable conclusion

for a species that is rather plastic in its use of cover types (Uehara 1990, Thompson 1997) in the absence of hunting pressure.

The Habitat Threshold is useful for highlighting areas of intact forest that may be most important for conserving bonobos in MLW. The Habitat Threshold may at first appear a cautious estimate of bonobo tolerance to fragmentation; however our nest surveys suggest that the Habitat Threshold likely is a plausible binary representation of bonobo-habitat suitability in MLW. For instance, no nests were found in the logging-impact area, which the Habitat Threshold essentially depicts as entirely fragmented, and fewer than 8% of nest blocks were found in areas with ED above the Habitat Threshold. The Habitat Threshold demonstrates the pervasive nature of human presence even in a remote area plagued by an unreliable transportation system (Hickey and Sidle 2006, USAID 2010). For an area boasting one of the last strongholds of bonobos in the world, the Habitat Threshold suggests that < 62% of MLW is sufficiently unfragmented for bonobo nesting. The Nest Threshold is a liberal threshold from a conservation perspective, resulting in a binary map showing more area with potentially suitably low levels of forest fragmentation. While decisions based on liberal thresholds may be criticized because they are prone to commission error (inclusion of unsuitable areas), they represent the best choice for describing all potential habitat given all observations. Further study of the relationship between ED and bonobo nest occurrence both in MLW and other areas is recommended to assess whether the relationship and relevant thresholds change temporally or regionally.

At a broad scale, ED is an effective landscape metric for estimating bonobo nest occurrence and therefore potential bonobo habitat. We suggest ED can be used to increase the efficiency of future bonobo surveys, by increasing survey effort in areas of lower ED and decreasing effort in areas of higher ED. Future surveys can continue to inform the relationship

between ED and nest occurrence and extrapolate to unsurveyed areas based on those ED values. We advise against zero effort in areas of higher ED because estimates of overall bonobo abundance or density rely on characterizing the areas of both low and high bonobo densities. Extrapolating high-density estimates across all areas would result in grave over-estimates of bonobo abundance in a given region. ED appears well suited for predicting bonobo occurrence in the MLW, an area with documented hunting impact on the bonobo population (Dupain and Van Elsacker 2001), and may extrapolate well to other areas of similar hunting pressure. However, the predictive value of ED may be weaker in areas where hunting pressure is relatively low because, in the absence of hunting, bonobos are relatively tolerant of open canopies and have been documented in some forest-savannah (fragmented) mosaics (Uehara 1990, Thompson 1997, Inogwabini *et al.*2008). Conversely, there could be specific locales within the bonobo range in which the forest is relatively intact, yet bonobos do not occur. This could be due to occasional targeted hunting of remote areas, or other habitat factors that remain unknown. However, these areas are rare enough in our data that they did not mask the relationship between nest presence and ED. In order to find these anomalous areas, and potentially discover other relevant controlling factors, it will be important to institute continued monitoring and communicate with biologists and local people alike. Further investigations may help elucidate this relationship.

We believe we are the first to quantitatively demonstrate that fragmentation can be an important predictor of species occurrence for primates while their habitat remains relatively intact. Across taxa, the preponderance of fragmentation studies focus on landscapes in the lower tail of the ED-*P* curve, showing that the dispersed loss of habitat is important in highly disturbed landscapes in which habitat occurs in isolated patches surrounded by a matrix of non-habitat (Andrén 1994, Fischer and Lindenmayer 2007, Arroyo-Rodriguez *et al.* 2008). Our study takes a

different approach, investigating the potential consequences of habitat fragmentation prior to the matrix transitioning from habitat to non-habitat (sometimes called perforation). We suspect that the mechanism by which fragmentation affects bonobo distributions is through increased bonobo avoidance of areas due to increased hunter access and increased hunting mortality near linear openings. Our study supports findings that hunting activity increases near openings and results in lower nest occurrence (Reinartz *et al.* 2008). Those linear openings in the forest habitat are effectively detected by remote sensing and measured by ED. We surmise that ED is most useful for landscapes with a preponderance of percent-habitat values in just one tail of the ED-*P* curve (Figure 2.1). In our landscape, the majority of areas were well over 80% forested, in the upper tail, where there exists a negative relationship between ED and percent habitat. While our analysis reinforces previous assertions of similarities among various measures of fragmentation and area (Hargis *et al.* 1998, Hargis *et al.* 1999), and supports the suggestion that fragmentation may impact bonobo habitat suitability (Kano 1984), it also quantitatively describes applicability of landscape-level fragmentation metrics for great ape habitat and assesses the impacts of fragmentation on habitat suitability.

Given the lack of studies of landscape-scale fragmentation metrics relevant to primates (Arroyo-Rodriguez and Mandujano 2009), we believe we have offered an approach that can be applied to other taxa. Fragmentation metrics can be developed for a given species by classifying habitat specifically with that species' needs in mind and by selecting a window size at the scale that the species likely responds to fragmentation (perhaps the scale of the species' homerange). These metrics can be ranked using field data to evaluate their utility in predicting species occurrence and made spatially explicit in maps. For land managers and conservation planners, we have outlined some defensible ways to identify thresholds of allowable canopy alteration for a

given species based on an evaluation of fragmentation values across the landscape and in different land use categories, in combination with levels of fragmentation where the species shelters. When delineating such thresholds we suggest employing species occurrence records that likely indicate areas of quality habitat rather than areas used in a transient manner. For example, we used nests where bonobos seek shelter for the night. The appropriate type of sign will depend on individual species' habits and needs. In addition, species-covariate relationships may change over time, especially as land use and climates shift, therefore repeated studies examining such relationships are warranted.

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Table 2.1. Landscape metrics used and their associated formulas[1].

Metric	Concept	Formula	Units
Edge Density	Fragmentation	length of forest edge/total area of window	m/ha
COHESION	Connectivity	$\left[1-\frac{\sum_{i=1}^{m}\sum_{j=1}^{n}p_{ij}}{\sum_{i=1}^{m}\sum_{j=1}^{n}p_{ij}\sqrt{a_{ij}}}\right]\left[1-\frac{1}{\sqrt{A}}\right]^{-1}(100)$	none
CONTAGION	Connectivity	$\left[1+\frac{\sum_{i=1}^{m}\sum_{k=1}^{m}\left[\left(P_i\left(\frac{g_{ik}}{\sum_{k=1}^{m}g_{ik}}\right)\right)\left[ln\left(P_i\right)\left(\frac{g_{ik}}{\sum_{k=1}^{m}g_{ik}}\right)\right]\right]}{2\ln(m)}\right](100)$	%
Class Areas	Area	area of forest within window	ha

[1]Formulas from Fragstats Official Website, variables modified to pertain to this study's moving-window analysis http://www.umass.edu/landeco/research/fragstats/documents/Metrics/Metrics%20TOC.htm

For COHESION:

p_{ij} = perimeter of patch *ij* in terms of number of cell surfaces

a_{ij} = area of patch *ij* in terms of number of cells

A = total number of cells in window

For CONTAGION:

P_i =proportion of the landscape occupied by patch type (class) *i*

g_{ik} =number of adjacencies (joins) between pixels of patch types (classes) *i* and *k* based on the double-count method

m = number of patch types (classes) present in the landscape, including the window border if present

Table 2.2. Rank, mean (±SE), and range of values of landscape metrics at nest sites: Edge density (ED), CONTAGION, COHESION, and Class Area (CA) each calculated on 3 different binary base forest-cover layers FOR (probability of being forested), RD (FOR with roads burned in), and RR (FOR with both roads and rivers burned in).

Rank	Metric	Units	Mean	(±SE)	Range	Total Prediction Error	True Positive Rate
1	ED - FOR	m/ha	1.18	0.25	0 - 11.7	27.91	85.48
2	ED - RD	m/ha	1.22	0.26	0 - 12.3	27.91	84.68
2	CONTAGION - FOR	%	98.2	0.37	98.1 - 100	27.91	84.68
3	COHESION - RD	none	99.87	0.03	98.6 - 100	29.45	84.68
4	ED - RR	m/ha	2.3	0.32	0 - 12.5	29.46	80.65
5	CONTAGION - RD	%	97.4	0.61	67.1 - 100	29.84	84.68
6	CA - RD	ha	1963	3.31	1783 - 1974	29.85	95.16
7	CA - FOR	ha	1969	1.1	1922 - 1974	29.85	85.48
8	COHESION - RR	none	99.7	0.04	98.2 - 100	29.85	79.84
9	CA - RR	ha	1944	4.64	1784 - 1974	30.23	83.06
10	COHESION - FOR	none	99.9	0.03	98.1 - 100	30.24	85.48
11	CONTAGION - RR	%	93.1	0.84	67.1 - 100	30.62	79.03

Rank is based first on leave-one-out cross-validation total prediction error (lower is better) and based second on true positive rate (higher is better). Note a tie in position 2 and a consistently high ranking for ED.

Table 2.3. Predictor variable, units, number of parameters (*K*), intercept, parameter estimate (±SE), odds ratio, and confidence interval for each candidate model predicting bonobo nest presence (based on the RD forest-cover layer) for the Maringa-Lopori-Wamba landscape, DRC.

Candidate Model	**Units**	***K*[a]**	**Intercept (±SE)**	**Estimate (±SE)**	**Odds Ratio[b]**	**Lower 95% CI**	**Upper 95% CI**
Edge Density	m/ha or km/10km^2	3	0.753 (0.168)	-0.255 (0.038)	0.775	0.72	0.833
CONTAGION	%	3	-9.28 (1.52)	0.0999 (0.016)	1.11	1.07	1.14
COHESION	None (0-<100)	3	-226.4 (35.5)	2.272 (0.356)	9.7	4.83	19.5
CA	ha	3	-31.8 (5.59)	0.016 (0.003)	1.017	1.011	1.022

[a]*K* is the sum of each model's single covariate parameter estimate, the intercept, and error term; each model has only one predictor variable.

[b]Odds ratios calculated as $e^{(estimate)}$ and odds ratios <1 indicate a negative relationship and are interpreted more easily by taking the inverse and stating "nest blocks are 1/ $e^{(estimate)}$ times" *less* likely to occur with each unit increase in the variable. Therefore nest blocks were (1/0.775)=1.3 times less likely to occur for each 1-km increase of edge per 10 km^2.

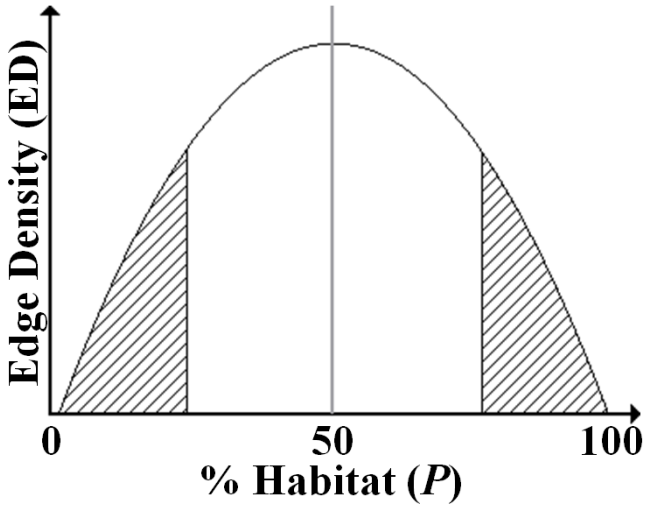

Figure 2.1. A hypothetical representation of the parabolic nature of edge density (ED) over the percent habitat (*P*) gradient. ED values tend to be lower for both low and high values of *P*.

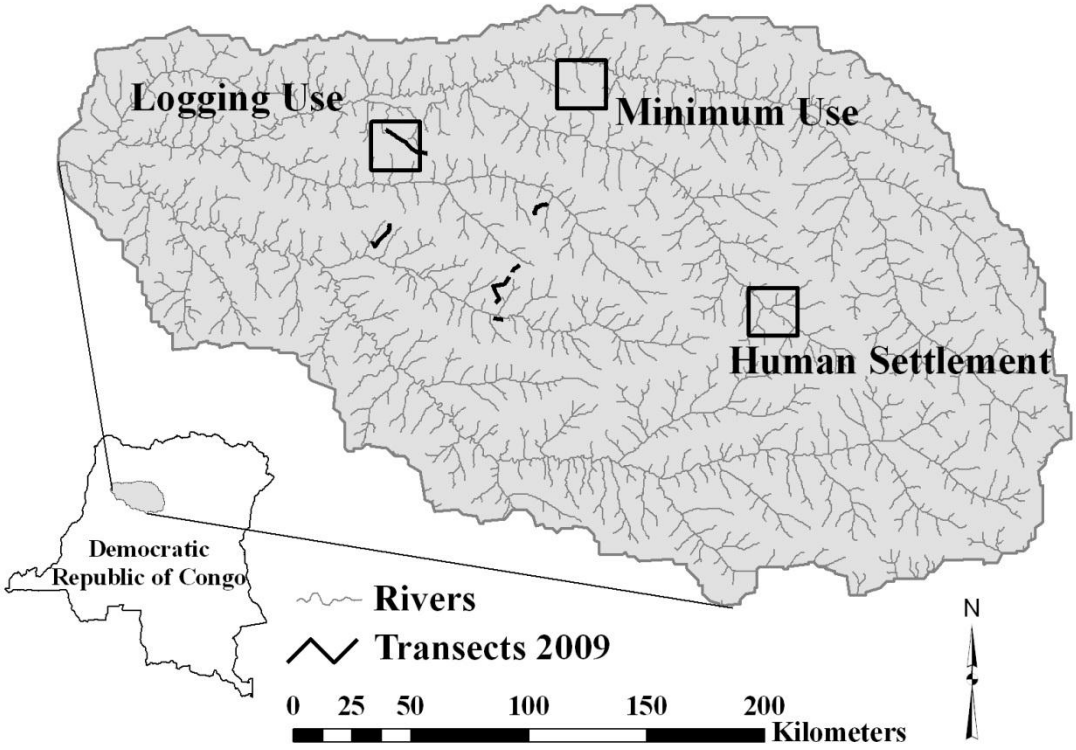

Figure 2.2. Maringa-Lopori-Wamba (MLW) landscape, Democratic Republic of Congo, selected focal areas, and location of line transects for bonobo nest surveys conducted in 2009.

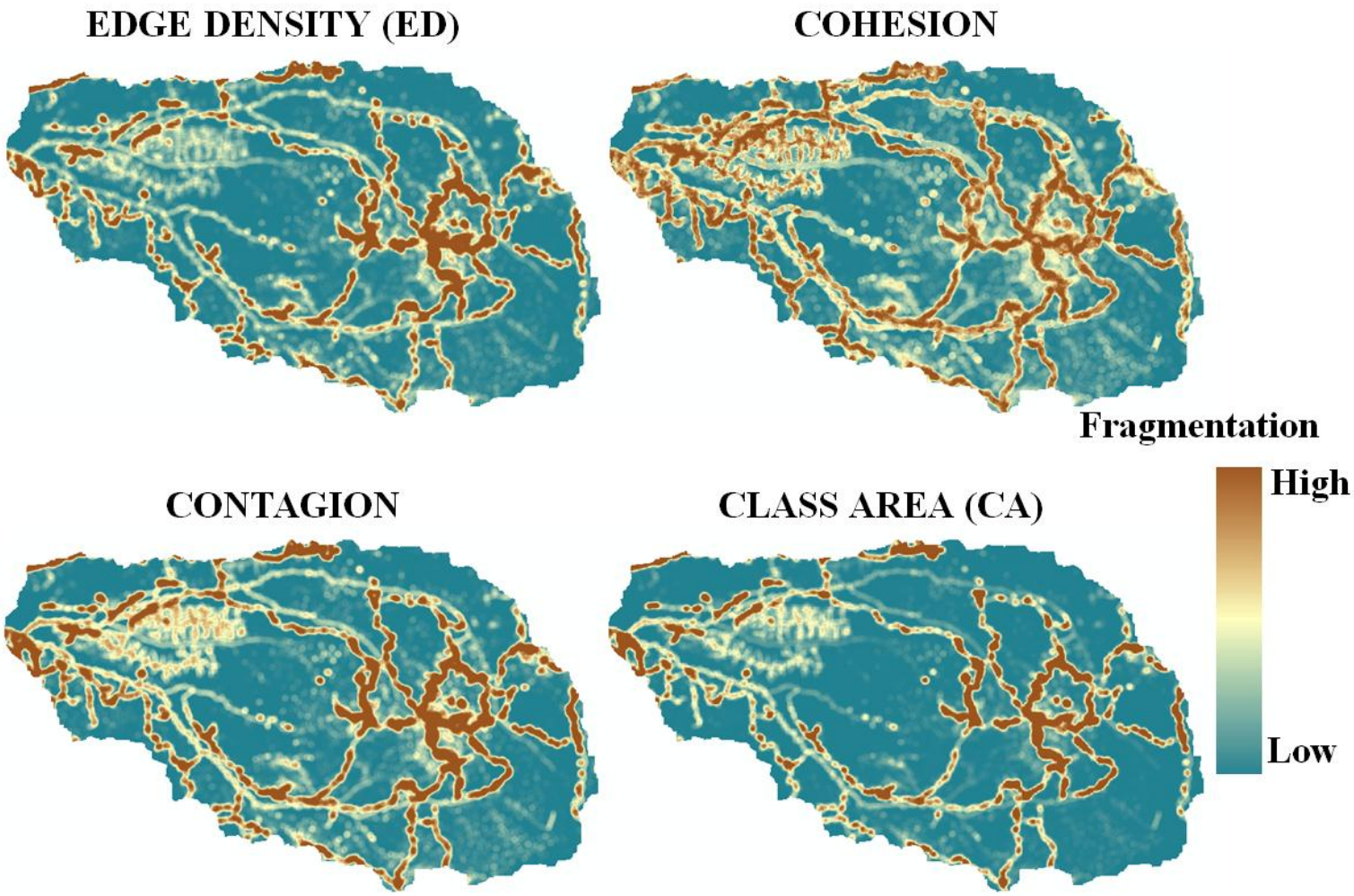

Figure 2.3. Maps of the four landscape metrics across the Maringa-Lopori-Wamba (MLW) landscape, Democratic Republic of Congo.

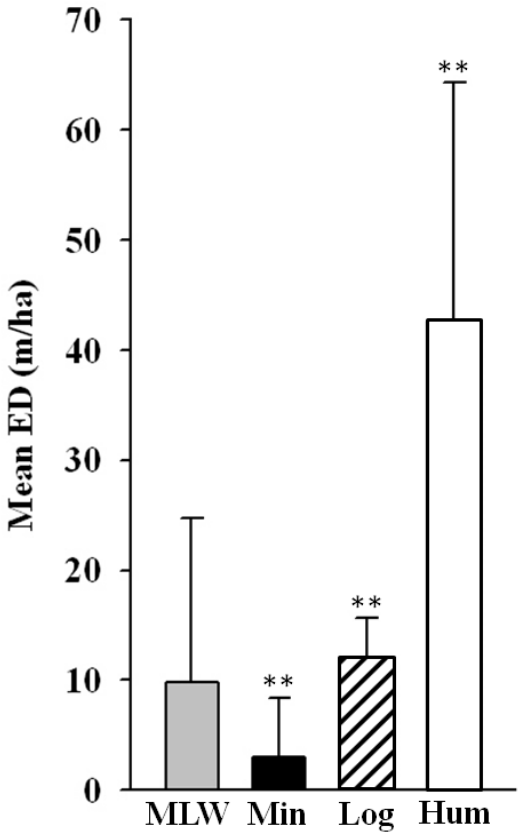

Figure 2.4. Mean ED (±SD) for the Maringa-Lopori-Wamba (MLW) landscape and selected focal areas. Focal area labels correspond as follows: Min=Minimum Use, Log=Logging Use, and Hum=Human Settlement; and (**) indicates significant difference from MLW at the $p<0.01$ level.

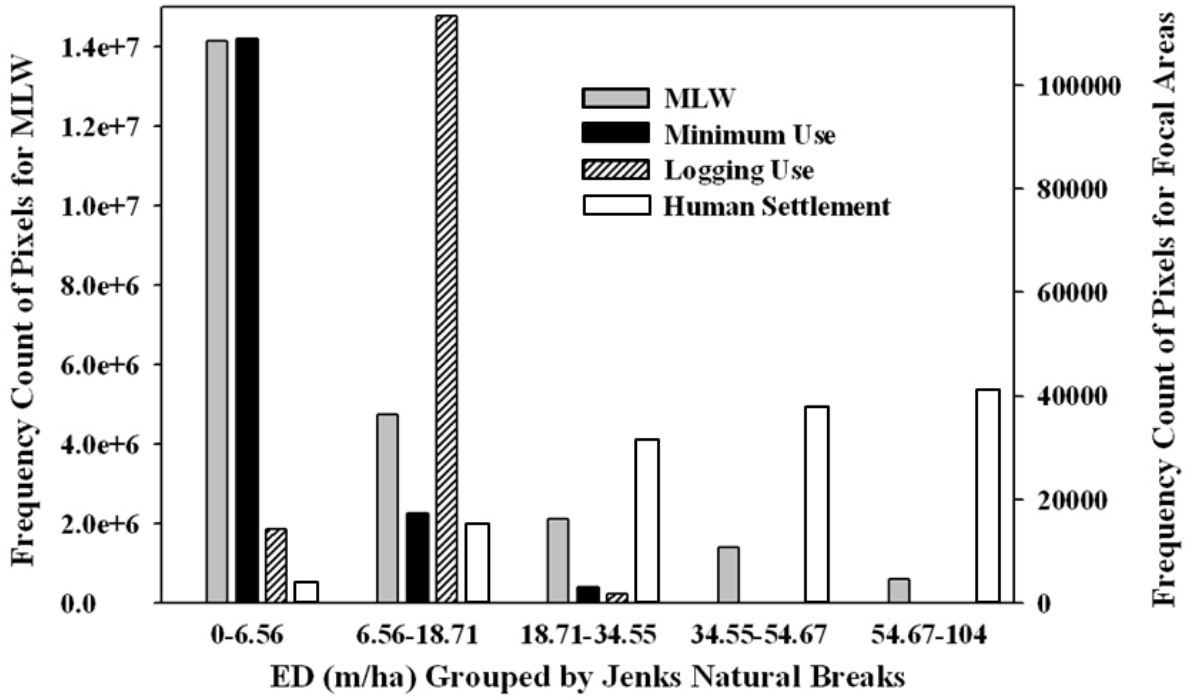

Figure 2.5. Frequency of edge density (ED) values (per pixel based on a 20-km^2 window around each pixel) for Maringa-Lopori-Wamba (MLW) and selected focal areas. Categories on the *x*-axis represent Jenks' natural breaks (Jenks 1967) for ED across MLW.

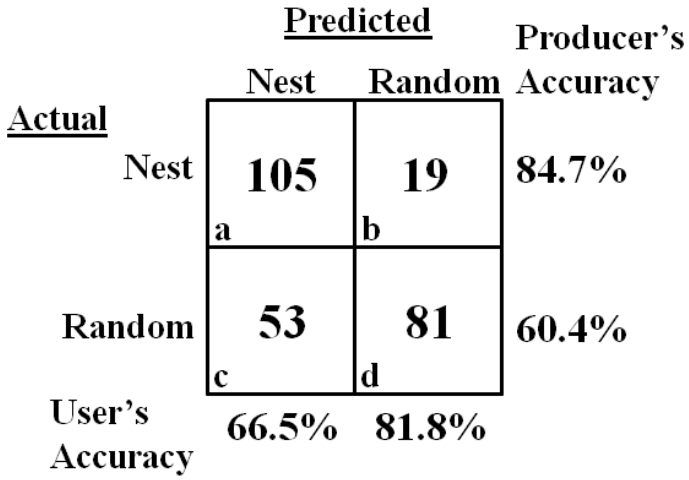

Figure 2.6. Confusion matrix showing classification accuracy of the ED-RD model. Box (a) reflects that 105/124=84.7% of known nest blocks were correctly classified. Box (c) highlights that the greatest source of error in this model is in misclassifying 53/134=39.6% of blocks as nest-blocks, when in fact, no nest was found (commission error).

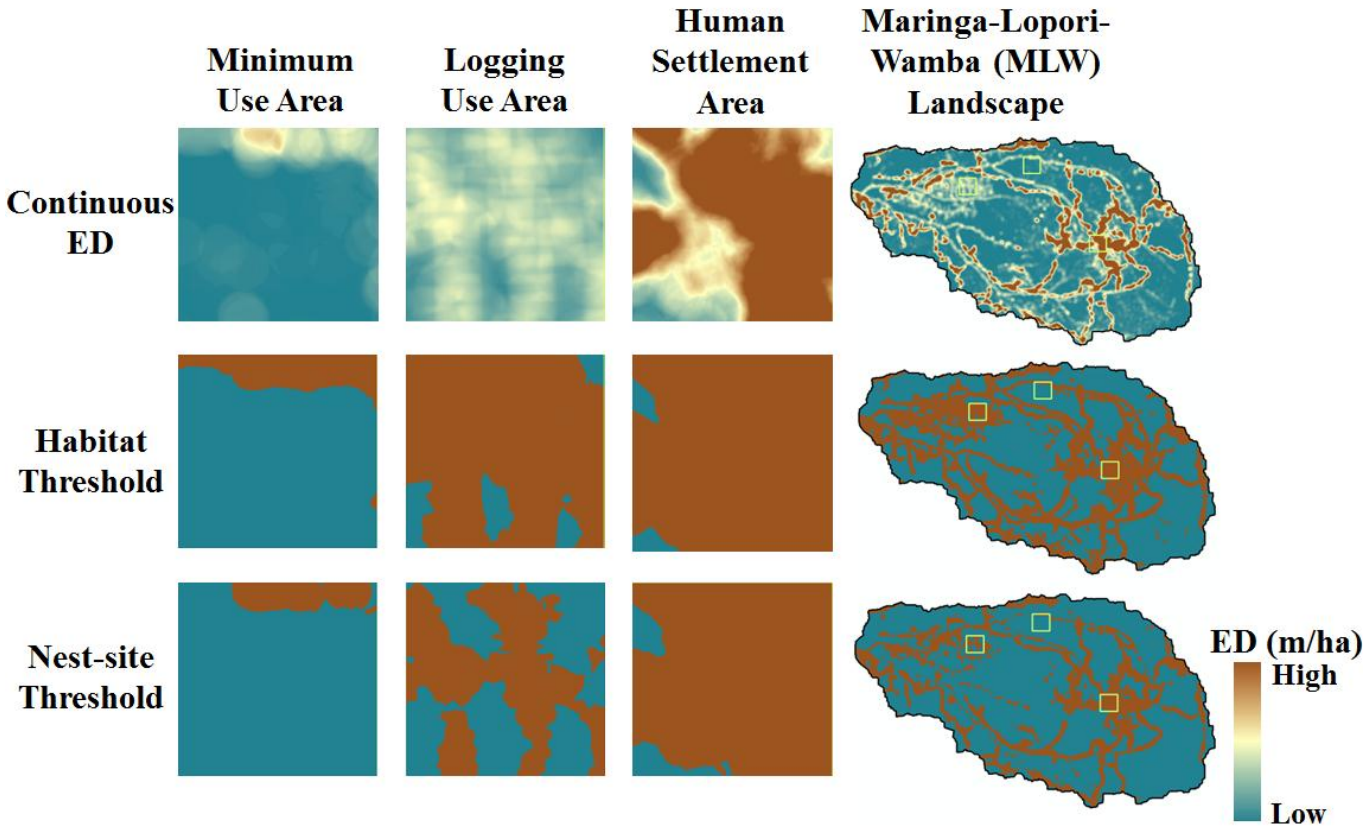

Figure 2.7. Focal areas highlight differences between continuous and thresholded edge density (ED) maps, and landscape-wide maps depict corresponding focal areas in light boxes from left to right: logging-use, minimum use, and human-settlement areas. Thresholds accentuate areas where ED may be too high for bonobo nesting.

CHAPTER 3

A SPATIALLY-EXPLICIT RANGEWIDE MODEL OF SUITABLE CONDITIONS FOR THE BONOBO (*PAN PANISCUS*) FOR CONSERVATION PLANNING[2]

[2] Hickey, J.R., J. Nackoney, N.P. Nibbelink, *et al.* 2012. To be submitted to *Diversity and Distributions.*

ABSTRACT

The bonobo (*Pan paniscus*), a great ape endemic to the lowland rainforests of the Democratic Republic of Congo, is threatened by habitat loss and hunting and is listed as Endangered by the IUCN™. There is an urgent need to create and implement effective bonobo conservation strategies, yet the bonobo's rangewide distribution is poorly known. Conservation planning requires a current, data-driven, rangewide map of the probable bonobo distribution as well as an understanding of the key attributes of areas more likely used by bonobos. Given that humans live and hunt in the bonobo range, it is worthwhile to quantify the effects of human disturbance and land-use change on bonobo habitat use. In an attempt to provide such information, we present the first rangewide suitability model for bonobos. We used a maximum entropy approach to species distribution modeling, in which attribute data associated with known locations of bonobo nests were used to predict locations of suitable conditions across the species' entire range. Classification accuracy, measured by the area under the curve (AUC), was high (0.82). Distance from agriculture and forest edge density (ED) were the best predictors of suitability, with test gains (goodness-of-fit) of 0.5 and 0.35, respectively, and resulted in a primarily threat-based model. Response curves indicated that bonobos were more likely to nest farther from agriculture and in areas of lower ED, suggesting that they avoid areas of higher human activity. The model results and maps can be used to determine core bonobo protection areas, identify priority areas for surveys, and increase our understanding of threats to bonobo populations.

INTRODUCTION

Wildlife conservation relies on understanding patterns of species occurrence. With the global human footprint ever growing and intensifying (Sanderson *et al.*, 2002), approximate delineations of species' ranges exclusively based on historic data are no longer enough for conservation and minimum-impact infrastructure planning. As such, spatially-explicit rangewide models that deliver fine-scaled information on suitable conditions are critical. Such models can inform land-use plans designed to maintain connected, viable populations of species. In the Democratic Republic of Congo (DRC), the annual human population growth is increasing rapidly - estimates range from 2.6% (UNDP, 2011) to 3.2% (USAID, 2010) - and has driven increased deforestation in areas of previously intact forest (Hansen *et al.*, 2008; OSFAC, 2010). Increased poverty from the collapse of the agricultural sector during and following DRC's recent civil war has also contributed to a rise in bushmeat hunting which remains a substantial threat to the viability of many game species (Draulans and Krunkelsven, 2002; Yamagiwa, 2003; Beyers *et al.*, 2011).

Bonobos (*Pan paniscus*) are great apes listed as Endangered on the IUCN Red List since 2007 (Fruth *et al.*, 2008). They are endemic to the lowland rainforests of DRC and are threatened by both habitat loss and hunting (IUCN, 2010). In order for conservation efforts to be successful, up-to-date information on the rangewide distribution of bonobos and an evaluation of their threats is required (Grossmann *et al.*, 2008). A bonobo conservation-action planning meeting was held in Kinshasa, DRC in January 2011, with a large group of bonobo experts, including representatives from DRC's Institution for the Conservation of Nature (Institut Congolais pour la Conservation de la Nature, ICCN). Several objectives for bonobo conservation were defined, including the promotion of strategic land-use management and conservation plans at local, regional and

national levels. Achieving this objective requires spatial information about the probability of bonobo occurrence in unsampled areas and the characteristics and drivers of habitat use.

To aid such efforts, we provide the first spatially-explicit bonobo rangewide suitability model. Model development began in a collaborative workshop held in Kinshasa immediately prior to the action-planning meeting. We further developed and refined the model during the following months. We used a maximum-entropy modeling approach (MaxEnt; Phillips *et al.*, 2006; Elith *et al.*, 2010) that combined bonobo nest locations with environmental layers to predict the spatial distribution of potentially suitable conditions. Recognizing that suitable conditions include food availability, shelter, and security from predation (including humans), we used a suite of environmental variables to model bonobo distribution and evaluated their relative importance in predicting bonobo occurrence. To date, spatial data classified into detailed categories relevant to bonobo foraging do not exist. We therefore focused on the presence of broad forest types where bonobos are known to nest, as well as abiotic factors likely influencing vegetation (and, indirectly, occurrence of forage species) and proxies for hunting pressure as measures of habitat security (Swenson, 1982). For the purpose of this paper, we define suitable conditions as those locations where bonobos nest, which necessarily includes avoidance of hunters.

MaxEnt is a modeling tool that uses presence-only occurrence data and has been found to perform favorably in comparison to other presence-only models (Elith *et al*., 2006; Hernandez *et al*., 2006). It has been widely applied in the species distribution modeling and mapping literature: primate examples include monkeys in Amazonia (Boubli and de Lima, 2009), slow lorises in Southeast Asia (Thorn *et al.*, 2009), and chimpanzees in West Africa (Torres *et al.*, 2010).

Using our model, we present a rangewide map of relative suitability for bonobos. The map and approach serve as a foundation to be refined in the future as improved classification of

vegetation, and other environmental data that can be used for predicting bonobo occurrence, become available. The DRC Government recognizes the need for sustainable land-use planning, and local and international non-government organizations have generated momentum toward achieving it (USAID, 2010). Our map and results will assist planning efforts by providing necessary information to prioritize areas for bonobo conservation.

STUDY AREA

The bonobo range, located in central DRC, is defined by the Congo River to the north and west, the Lualaba River to the east, and the Kasai/Sankuru Rivers to the south (IUCN, 2010). Although the western portion of the range is currently thought to be discontinuous, we included the entire area in our model because the collective knowledge on bonobo occurrence, especially in unsurveyed areas, is still expanding. We therefore developed a contiguous boundary based initially on the IUCN (2010) range and then expanded it to encompass all known bonobo occurrences southward to the Kasai River, thereby eliminating any isolated pockets (Fig. 3.1).

DATA AND METHODS

Bonobo data

Multiple entities collected the presence-only bonobo data used in this model. These data were compiled as part of the Apes, Populations, Environments, and Surveys (A.P.E.S.) database maintained by the IUCN/SSC Primate Specialist Group (PSG) and managed by the Max Planck Institute for Evolutionary Anthropology. The A.P.E.S. database provides a global picture of the distribution and status of great apes and informs their long-term management and conservation strategies. During the Kinshasa workshop, we evaluated the presence-only data and performed quality assessment and control prior to input into the model. We used bonobo nest locations from the A.P.E.S. database, rather than all signs (e.g. feeding remains or tracks) in order to characterize

habitat where bonobos nest rather than where they might move through in a transient manner. Numerous teams collected data along either randomly- or systematically-located line transects or recce walks; the latter followed the path of least resistance and focused on areas where bonobo signs were found. Because bonobo nests and nest sites tend to be clustered, we reduced the effects of spatial auto-correlation by aggregating our individual nest or nest-site locations to 100 x 100 m blocks (the same resolution as our final environmental predictor layers). A block containing one or more nests or nest sites was termed a *nest block*. The block size corresponds well to the scale of nest groups because the risk of a single nest group being split between two blocks is low as the gap between nests within a group tends to be 30 m or less (Mulavwa *et al.,* 2010). We compiled data for 2,364 nest blocks distributed across the bonobo range (Fig. 3.1).

Predictor Variables

We collaboratively developed and evaluated a suite of environmental predictors thought to be relevant to bonobos. MaxEnt allows for the incorporation of a diverse range of environmental predictor variables (hereafter referred to as "predictors" or “environmental layers”) including biotic, abiotic, and threat-based data. However, MaxEnt requires that data values exist for each pixel across the entire modeled range. Factors influencing bonobo presence, such as detailed vegetation layers and understory information (including bonobo forage species), are not classified and mapped for the bonobo range. This is likely due to the vast size and extreme inaccessibility of the region, a history of highly localized research effort, and the sheer logistical and economic challenges to ground truth remotely sensed data in Central Africa.

To construct this model, we focused on two broad biotic predictors (percent forest and presence of intact forest), selected abiotic factors that may influence vegetation (and hence, forage), and various measures of potential hunting pressure. The environmental layers came from

a wide variety of sources with varying resolutions and expected influence on bonobos (Table 3.1). We resampled the environmental layers to 100-m resolution in ArcGIS in order to standardize the pixel size. The Africover data (FAO, 2000) contained six landcover categories: agriculture, broadleaved rainforest, swamp rainforest, shrub, urban, and water. Because we found that most nest blocks (99.9%) were located in just two forest covertypes (broadleaved rainforest and swamp rainforest), we re-classified these data into percent forest based on a 3 x 3 cell neighborhood of 100-m cells (=0.09 km^2) using FRAGSTATS 3.3 (McGarigal *et al.*, 2002). This neighborhood analysis addressed potential GPS error and decreased the possibility of misclassification of any given cell. Although we could have used broadleaved forest (terra firma) exclusively, we included swamp forest in the percent-forest variable because there is evidence that bonobos also nest in swamp forest. While bonobos nest in terra-firma forest more often (Reinartz *et al.*, 2008; Mohneke and Fruth, 2008), Mulavwa *et al.* (2010) reported 13% of nest groups in swamp forest, suggesting that a model predicting suitable conditions for bonobos must include this landcover type.

MaxEnt Modeling

We used a machine-learning approach called maximum entropy (MaxEnt; Phillips *et al.* 2006; Elith *et al.* 2010) to develop a relative suitability map (Guissan and Thuiller, 2005) for bonobos based on relationships between nest-blocks and the above environmental predictors. MaxEnt (version 3.3.1) is a modeling tool that predicts species occurrence based on presence-only data. It does not require known absences; instead, MaxEnt relies on random background points to characterize the range and variation of values for each environmental layer across the study area. Using the "species with data" (SWD) format and 10,000 random background points, MaxEnt compared the environmental values of nest blocks to the full range of environmental values

observed throughout the bonobo range to predict probability of suitable conditions in unsurveyed areas (Elith *et al.,* 2010). It is noteworthy that MaxEnt performs best with relatively broad sampling coverage within the area of interest (Phillips *et al.,* 2009). Although there was clustering in nest locations where sampling intensity was high, nest-block locations are well-distributed throughout the bonobo range (Fig. 3.1).

Using presence-only data can sometimes produce results that are geographically biased to the regions near the presence points (Phillips *et al.,* 2009; Phillips, 2008). This effect can be most pronounced if those areas are highly surveyed relative to the full dataset (Phillips *et al.,* 2009). To test for such bias, we ran iterative models withholding nest-block locations from specific regions to evaluate how well each reduced-data model performed in the area of withheld nest locations. This procedure informally evaluated the sensitivity of the models to potential bias from highly sampled sites. Specifically, we tested a succession of separate models, independently withholding nest data from each of the following highly-sampled regions: Maringa-Lopori-Wamba (MLW), Tshuapa-Lomami-Lualaba (TL2), and Salonga National Park (SNP) (Fig. 3.1a, 3.1b, and 3.1c, respectively). We also ran another series of models that each used only the data from one intensively-sampled region at a time, plus a model using only data from a lightly sampled area (39 nest blocks) called Lac Tumba (LT) (Fig. 3.1d). These sensitivity tests allowed us to evaluate how well models built with presence data from each region predicted the other regions of known occurrence and whether the relative importance of the different predictor variables changed based on the region from which the presence data originated.

We varied the suite of included environmental layers to test their predictive performance and to refine their selection based on diagnostics (explained below). We rejected predictors exhibiting too narrow a range of values because they added little discerning capability to the

models (e.g. certain global or continental datasets, such as soil type, were mapped at such coarse resolutions that only one value dominated the entire bonobo range). For each MaxEnt analysis in the series, we used a random 70% of the nest blocks as training data to build the model and withheld 30% to independently test model accuracy.

A common method for evaluating the classification accuracy of MaxEnt models is with the area under the curve (AUC) of a receiver operating characteristic (ROC) plot (Phillips *et al.,* 2006). An AUC of 0.5 represents a prediction no better than random, whereas a theoretically perfect prediction would approach an AUC of 1, with no errors of omission or commission. Omission and commission error, or false-negative and false-positive prediction respectively, are used to calculate sensitivity and specificity. Traditionally, a graph of the true positive rate (sensitivity) on the y-axis and the false positive rate (1-specifcity) on the x-axis gives the AUC. MaxEnt, however, calculates the AUC using the fractional predicted area on the x-axis (Phillips *et al.,* 2006), resulting in a theoretical maximum equal to [1 – (predicted area/2)] (Wiley *et al.,* 2003). This adjustment accounts for the fact that the background points are not true absences and therefore do not indicate false positives. Standard deviation of the test AUC provided an estimate of significance (DeLong *et al.,* 1988; Phillips, 2006).

We also ran a jackknife analysis in MaxEnt to determine the relative contribution of each environmental predictor to the models' performance. In this procedure, MaxEnt removes one predictor and runs the model once on the individual predictor and again on the remaining predictors. With this approach, MaxEnt calculated the difference in the training and test gains of each predictor alone, the model without that predictor, and the full model with all predictors included. *Gain* is closely related to deviance, a measure of goodness of fit used in generalized additive and generalized linear models; it starts at 0 and increases asymptotically during the

model run (Phillips, 2006). Training and test gains relate to training and test data, respectively. High test gains reflect predictor variables that better predict locations not used to build the model (test data). Because MaxEnt does not generate conventional parameter estimates as in logistic regression, this jackknife procedure helps to describe the relative contribution of each variable to the full model (Phillips, 2006). To develop the final model, we removed environmental predictors that contributed negligibly to prediction (low gains). To avoid multicollinearity, we calculated Pearson's correlation coefficient, *r*, and removed predictor variables that were strongly correlated ($r \geq 0.49$). For binary suitability maps, we selected the "maximum sensitivity plus specificity" threshold because it balances omission and commission errors thereby generating neither overly cautious nor overly optimistic predictions regarding suitable conditions.

RESULTS

MaxEnt Modeling

The final output of the MaxEnt model (Fig. 3.2) highlights the areas most likely suitable for bonobos based on the final model containing distance from agriculture, ED, percent forest, and distance from river. The jackknife analyses showed that the first three of these were the best predictors of bonobo nest presence (Table 3.2 and Fig. 3.3). We included distance from river in the final model because it increased model accuracy and was not correlated with the other three predictors. Each of the predictors was threat-based except percent forest. Distance from agriculture contributed the most to the final model and to all models with one region withheld, making it the most important predictor. In the final model, approximately 28% (156,211 km^2) of the bonobo range was predicted suitable based on the maximum sensitivity plus specificity threshold. This cut-off value was 0.3, producing a maximum classification accuracy when values

greater than 0.3 were classified as suitable. Within the area of suitable conditions, 28% (43,836 km^2) was located in official protected areas.

Predictor-exclusion rules rejected certain variables from the final model as follows. We removed forest-loss variables because they contributed negligibly (training gains < 0.05 each). Distance from agriculture and distance from roads were highly correlated (Pearson's r=0.72), and therefore we removed the weaker predictor of the two, distance from roads. Nevertheless, distance from roads was a very strong predictor of bonobo nest occurrence, with nests more likely to occur farther from roads. Presence of intact forest was negatively correlated with edge density (ED) (r=-0.55) and hence was rejected, leaving the variable with the highest test gain, ED, as the only remaining forest pattern metric. We removed soil and lithology because they varied too little in their values throughout the range. Similarly, elevation and precipitation exhibited a narrow range of values, 145-672 m and 118-179 mm/month, respectively. Because of this, MaxEnt over-fit the model to these two variables, creating highly complex relationships that were not biologically defensible, so we omitted them.

Training and test AUCs (0.82 and 0.80, respectively) indicated strong prediction accuracy for the final model. MaxEnt calculated the theoretical maximum test AUC [1 – (predicted area/2)] of our data as 0.816. The small standard deviation (±0.007) of the test AUC confirmed the model performance was significantly better than random (AUC = 0.5). In addition, the series of models for which we removed data from one highly-sampled region at a time resulted in maps that still predicted the withheld regions as likely suitable (not shown). This confirmed that the final model (1) predicted suitable conditions beyond regions of known occurrence and (2) is robust to missing data.

Models in the withhold-one-region series generally agreed and supported the final model, whereas models built using region-specific nest blocks showed some noteworthy differences in terms of both transferability and predictor variable importance. For comparison purposes, we applied the final model's threshold of 0.3 to all region-specific models (Figure 4). The models built with MLW-only (Fig. 3.1a) and SNP-only (Fig. 3.1c) data agreed most with the final model (44.6% and 63.5% spatial overlap, respectively). The SNP model predicted similarly to the MLW model (overlapping 91% of the MLW model), yet the SNP output had larger areas of high suitability. The MLW model predicted 13% of the range as suitable while the SNP model predicted 18%. The TL2-only model was the most liberal, predicting nearly 44% of the range as suitable. The LT-only model was the most dissimilar of the four region-specific models; it predicted only 11% of the range as suitable, and those locations were nearly the spatial inverse of the final model's prediction with only 8% spatial overlap. Of the four predictor variables, distance from agriculture had the highest test gain for all models except the MLW-only model, for which ED was higher. ED was one of the top two predictors for all region-specific models except TL2, which was more influenced by percent forest than by ED. Distance from river had test gains between 0.14 and 0.24 for all region-specific models except the TL2 model, which had a test gain of 0.06.

The response curves (Fig. 5) show the relationship between each predictor and suitability of conditions for bonobos based on the final model. As expected, distance from agriculture and distance from rivers were both positively correlated with bonobo occurrence. This pattern may be indicative of a threat-based response in which higher hunting pressure occurs near concentrations of humans (indicated by agriculture) and access points (indicated by rivers). ED was negatively correlated with bonobo occurrence, suggesting that bonobos tend to nest in areas of low ED rather

than highly fragmented forests. Percent forest was a broad-scale predictor, positively correlated with bonobo occurrence.

As described earlier, elevation was excluded from the final model; however, prior to removal, it too served as a broad predictor suggesting that bonobos tend to occur above approximately 400-m elevation. When elevation was included in the model, the mapped output predicted large swaths of terra-firma forest in the south-west and a smaller area in the north-west of the range as *un*suitable. Yet, when elevation was excluded from the model, the output depicted these same regions as suitable (Fig. 6). Based on our knowledge of bonobo ecology, we find no support for this type of elevation-related limitation to their distribution given the presence of appropriate vegetation and absence of potential threats.

DISCUSSION

The results from our iterative modeling approach strongly suggest that threats associated with human activity (distance from agriculture, distance from roads, forest fragmentation, and distance from river) drive bonobo distributions. We view these predictors as proxies of hunting impact. Areas closer to agriculture and roads are closer to human populations who tend to hunt in the surrounding forest (Robinson, 1996; Hart *et al*., 2008). Roads and navigable rivers provide human access to areas that would otherwise likely be less vulnerable to hunting (Wilkie *et al*., 2000; Blake *et al*., 2009), as such features are major transport conduits to markets. Edge density (ED) distills the information of forest fragmentation from agriculture, logging, major rivers, and roads into a single metric that relates to hunter accessibility. Very likely, it is the poaching associated with these metrics that is the single common threat influencing bonobo occurrence. At the regional/local scale, however, there will be some exceptions to this general rule due to cultural taboos against eating bonobos. Such taboos are in a state of flux due to changing values

associated with immigrant populations (Fruth *et al.,* 2008); therefore poaching of bonobos may begin to occur in new areas, further magnifying this threat.

In the current model, the threat-based variables were better predictors of suitability for bonobos than were biotic and abiotic factors. However, this could be due to the fact that there were more datasets available describing human threats, in the required raster format, covering the correct geographic extent, and with adequate spatial detail, than were available for biotic and abiotic factors. Because hunting persists throughout most of the bonobo range, including areas that are legally protected (Dupain and Van Elsacker, 2001; Hart *et al.*, 2008), it is not possible to determine the environmental variables that would predict suitable conditions in the absence of hunting. Finer-scale analyses of relative hunting pressure are recommended to untangle these effects. While distance from roads was not included in the final model due to multicollinearity with distance from agriculture, distance from roads was in fact one of the strongest predictors of bonobo nest occurrence (second only to the correlated variable, distance from agriculture). As such, proximity to roads should also be considered an important threat to bonobos. We recommend repeating this study's approach when more detailed biotic and abiotic data relevant to bonobos become available.

The first bonobo conservation action plan (Thompson-Handler *et al.,* 1995) recognized that very little was known about bonobos and outlined an expansive area that needed to be surveyed to determine bonobo distribution, abundance and the environmental factors affecting bonobo presence. Here, we show the results of a comprehensive compilation of bonobo nest data collected since then and offer a current rangewide bonobo distribution model (Fig. 3.2) that can be used to inform future bonobo conservation actions and plans. Due to its rangewide, raster-based requirements, the model provided here does not benefit from finer-resolution data or the

more detailed understandings of local areas well-known to particular researchers. Instead, this type of knowledge of bonobo occurrence can be used in combination with the prediction map on a case-by-case basis. Certainly, future modeling will benefit from higher resolution environmental data, particularly for vegetation. While no model is perfect, we consider this model to be the best current rangewide spatial depiction of potentially suitable conditions for bonobos.

When building predictive models, it is important to critically consider classification accuracy (AUC). In some previous studies (Phillips *et al.*, 2009; Veloz, 2009), MaxEnt occasionally produced inflated measures of AUC, a problem that was most severe with small sample sizes in which samples were geographically clumped in a few isolated portions of the modeled area (Anderson and Gonzalez, 2011). For such studies, the data were biased by the characteristics found in those limited geographic areas, yet high accuracies were reported (all AUCs>0.9 when extrapolating to areas ≥100 km from known presences, VanDerWal *et al.*, 2009). Suggestions for corrective action have included restricting the geographic distribution of the background points used by MaxEnt to surveyed areas in order to match potential bias in the presence-only data (Phillips *et al.*, 2009). Our sensitivity test of a model in which we used LT-only data (39 nest sites) underscored the caution needed when modeling large areas with small presence-only datasets (Fig. 3.4d), because the LT-only output is implausible given the other known nest locations throughout the range. In contrast, the strength of the full dataset used in our final model is that the data are numerous (>2,000 nest blocks), the points span the entire modeled area, clusters of those points cover vast expanses, and surveyed regions represent a broad portion of each predictor's range of values. Due to these characteristics, we did not restrict background points to surveyed areas but instead used 10,000 random points distributed throughout the entire range. We interpret the test AUC (0.80) of this study to be biologically reasonable based on the

input data and, after iterative modeling, find no evidence that is inflated. The high AUC demonstrates that the model exhibits high classification accuracy and therefore is likely to be useful in predicting areas of relative suitability.

The final model predicted numerous unsampled areas as likely suitable for bonobos, suggesting that this model is not overly biased to vicinities near presence points. The succession of test models built by sequentially removing presence data from each highly-sampled region (i.e., MLW, TL2 and SNP) demonstrated high spatial overlap with each other and with the final model. Such agreement further increases our confidence in the model's portrayal of suitable conditions for bonobos. Finally, our series of test models built using just one highly-sampled region at a time confirmed that the full set of compiled presence data sufficiently portray the range of conditions (described by the predictors) that bonobos will generally tolerate, given that humans are part of the landscape.

However, all models are simplified interpretations of the real world with inherent error. Because of the spatially-explicit nature of MaxEnt, predictor variables were restricted to those for which data existed across the entire range. Moreover, there was uncertainty regarding the best way to compute the percent-forest variable because <2% (n=2364) of nest sites were located in swamp forests, yet there is evidence that, in addition to terra-firma rainforest, bonobos do nest in swamp forests more frequently than indicated by the rangewide dataset (Mulavwa *et al.,* 2010; Reinartz *et al.,* 2008; Mohneke and Fruth, 2008). Specifically, Mulavwa *et al.,* (2010) reported 13% of nests in swamp forest, and the landcover data (FAO, 2000) used in the current study classifies 20% of the range as swamp forest, suggesting that bonobos may nest in swamp forest at rates comparable to its availability. We concluded that swamp forest is underrepresented in

survey effort, partially due to its sampling difficulty, and therefore included it in our computation of percent forest.

The iterative MaxEnt modeling approach identified the most important factors determining the current bonobo distribution, namely: distance from agriculture, ED, and percent forest. Distance from agriculture was the strongest predictor of bonobo presence, with suitability increasing farther from agriculture. The MLW-only model was an exception, where the test gain for ED was highest. This difference appears to be due to the lack of areas within MLW located extremely far from agriculture, such that a model built on MLW-only data had limited transferability to locations that are extremely far from agriculture (dark regions at center of SNP Fig. 3.4a). Another exception was a relatively low predictive power for ED and distance from river in the TL2-only model. The higher amount of woodland-savannah interface in TL2 likely results in higher ED independent of hunting pressure, greater importance of percent forest, and/or potentially lower hunting pressure by the TL2 community. These varied results demonstrate both the geographic variation of factors determining bonobo presence and the importance of using well-distributed presence-only data when extrapolating to broad areas across the entire range.

The final suitability map, complemented by maps of the threats outlined here, provides a necessary starting point for developing creative on-the-ground actions needed to maintain viable bonobo populations. For instance, the map identifies certain unsurveyed areas as potentially suitable and that may be important for bonobo conservation. Such areas may either currently harbour unsurveyed bonobo populations or support a natural expansion of the current bonobo distribution. Additional bonobo surveys in these areas (highlighted in Fig. 3.2) are especially important. Here, the best predictors – distance from agriculture and ED – represent habitat loss in addition to hunter access. Others have noted the importance of habitat loss and fragmentation to

primate populations (Arroyo-Rodriguez and Mandujano, 2009). Therefore, where possible, we recommend any future agriculture, logging or infrastructure development concentrate in areas of least suitability and avoid areas of high suitability. Further, we recommend increased enforcement of current wildlife protections and increased efforts to provide alternative livelihoods to human communities within the bonobo range. Overall, we urge that priority actions focus on reducing bonobo mortality caused by hunting. We hope our analysis will contribute significantly to the development of land-use management plans aimed at protecting highly suitable areas, reducing threats to bonobos, and promoting conservation and sustainable natural resource management throughout the bonobo range.

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Table 3.1: List of environmental predictor variables originally used and those in the final model predicting relative suitability of conditions for bonobos rangewide, Democratic Republic of Congo.

			Expected Relationship				
Category	**Name**	**Description**	**Influence forage**	**Forage availability**	**Security from hunting**	**Bonobo Presence**	**Source**
Forest metrics	Percent forest*	Percentage of broadleaf terra-firma and swamp forest in a 9-cell neighbourhood (=0.09 km^2) reclassified from 6 landcover types	Yes	+	+	+	FAO 2000
Forest metrics	Intact forest	Presence of blocks of forest >500 km^2	Yes	+	+	+	Potapov *et al.* 2008
Forest metrics	Forest edge density*	A measure of forest fragmentation at 57-m resolution, then resampled up	Yes	U	-	-	Hickey *et al*. 2012
Climate	Monthly Mean Precipitation	mm/month	Yes	+	No	+	Hijmans *et al.* 2005
Terrain	Elevation	1-km Digital Elevation Model	Yes	U	U	U	USGS 2000
Terrain	Soil lithology	Surface rock type	Yes	U	No	U	van Engelen *et al*. 2006
Terrain	Soil types	Dominant soil types	Yes	U	No	U	van Engelen *et al*. 2006
Terrain	Compound Topographic Index	From HYDRO1k Elevation Derivative Database	Yes	U	No	U	USGS 2000
Terrain	Distance from rivers*	Distance to nearest river or stream in km calculated from HYDRO1k Elevation Derivative Database	Yes	U	+	+	USGS 2000
Human Impact	Distance from agriculture*	Distance to nearest agricultural complex in km as reclassified from landcover types	Yes	+	+	+	FAO 2000
Human Impact	Distance from roads	Distance to nearest road in km	No	U	+	+	WRI 2010
Human Impact	Presence of forest loss	Locations of areas experiencing deforestation between the years 1990-2000 and 2000-2010	Yes	U	-	-	OSFAC 2010
Human Impact	Distance to forest loss	Distance to nearest areas experiencing deforestation between the years 1990-2000 and 2000-2010	Yes	U	+	+	OSFAC 2010

* Retained in final model
Yes = predictor variable expected to influence the location of bonobo forage species
No = predictor variable not expected to relate to the life-history component listed
U = Relationship unknown
\+ = Positive correlation expected between predictor variable and mechanism influencing bonobo presence
\- = Negative correlation expected between predictor variable and mechanism influencing bonobo presence

Table 3.2: MaxEnt diagnostics for each predictor variable modeling relative suitability of conditions for bonobos rangewide using only that predictor variable. Gain is a measure of relative goodness-of-fit (Phillips 2006). An AUC of 1 would be perfect prediction whereas 0.5 would be no better than random.

Predictor Variable	Training Gain	Test Gain	AUC
Distance From Agriculture	0.58	0.50	0.77
Edge Density	0.34	0.35	0.73
Percent Forest	0.16	0.15	0.58
Distance From River	0.10	0.08	0.6

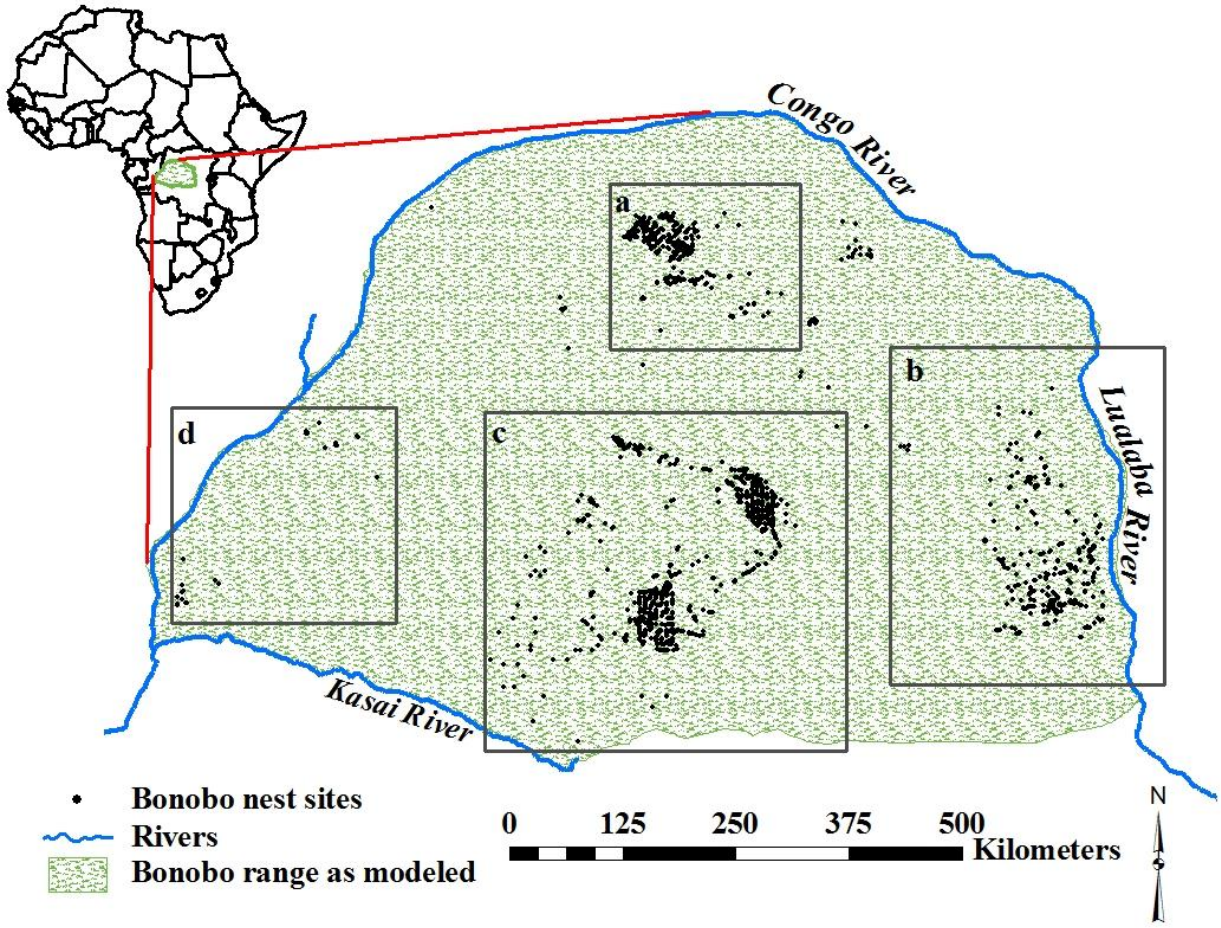

Figure 3.1. Map of the bonobo range as defined for the purpose of this effort to model suitable conditions for bonobos rangewide. All wild bonobos inhabit the area south of the Congo River, Democratic Republic of Congo. Specific regions referred to in the text correspond to the boxes: a) Maringa-Lopori-Wamba Landscape, b) Tshuapa-Lomami-Lualaba Landscape c) Salonga National Park, and d) Lac Tumba, respectively.

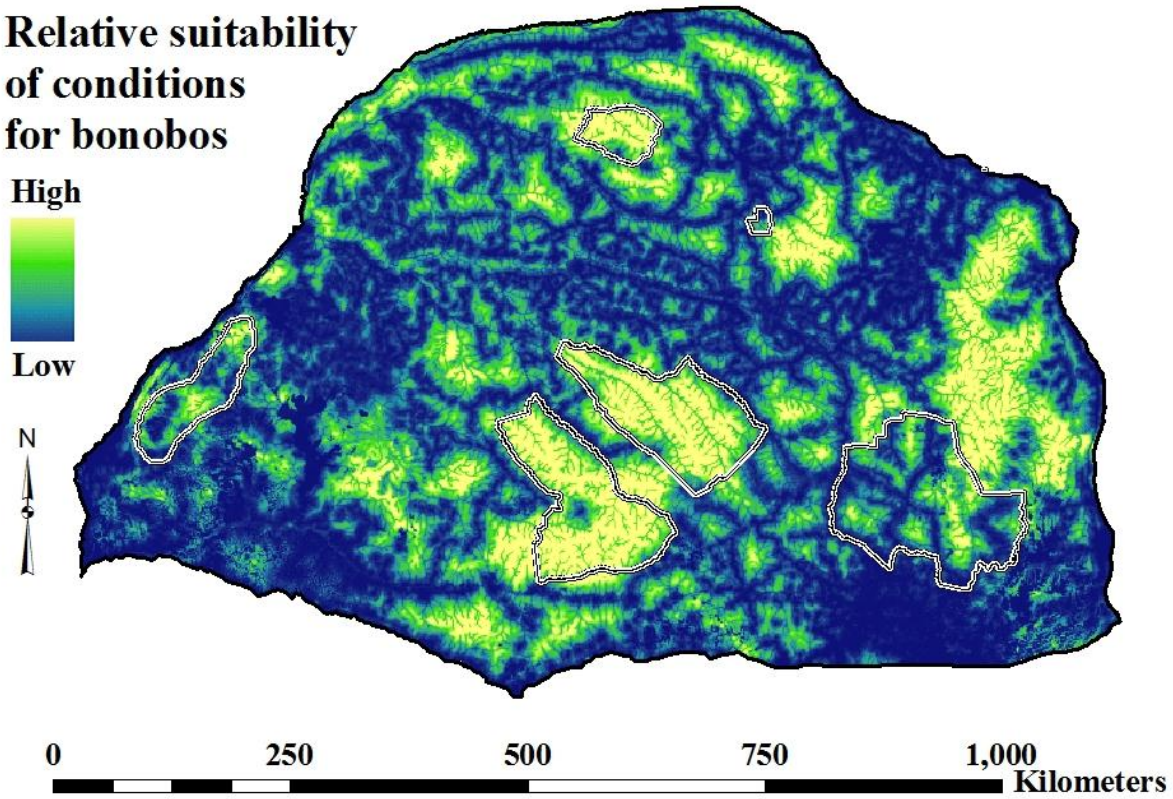

Figure 3.2. Final rangewide map of suitable conditions for bonobos, based on bonobo nest blocks and the strongest non-correlated predictor variables using a maximum-entropy approach. The polygons denote boundaries of official protected areas at the time of writing.

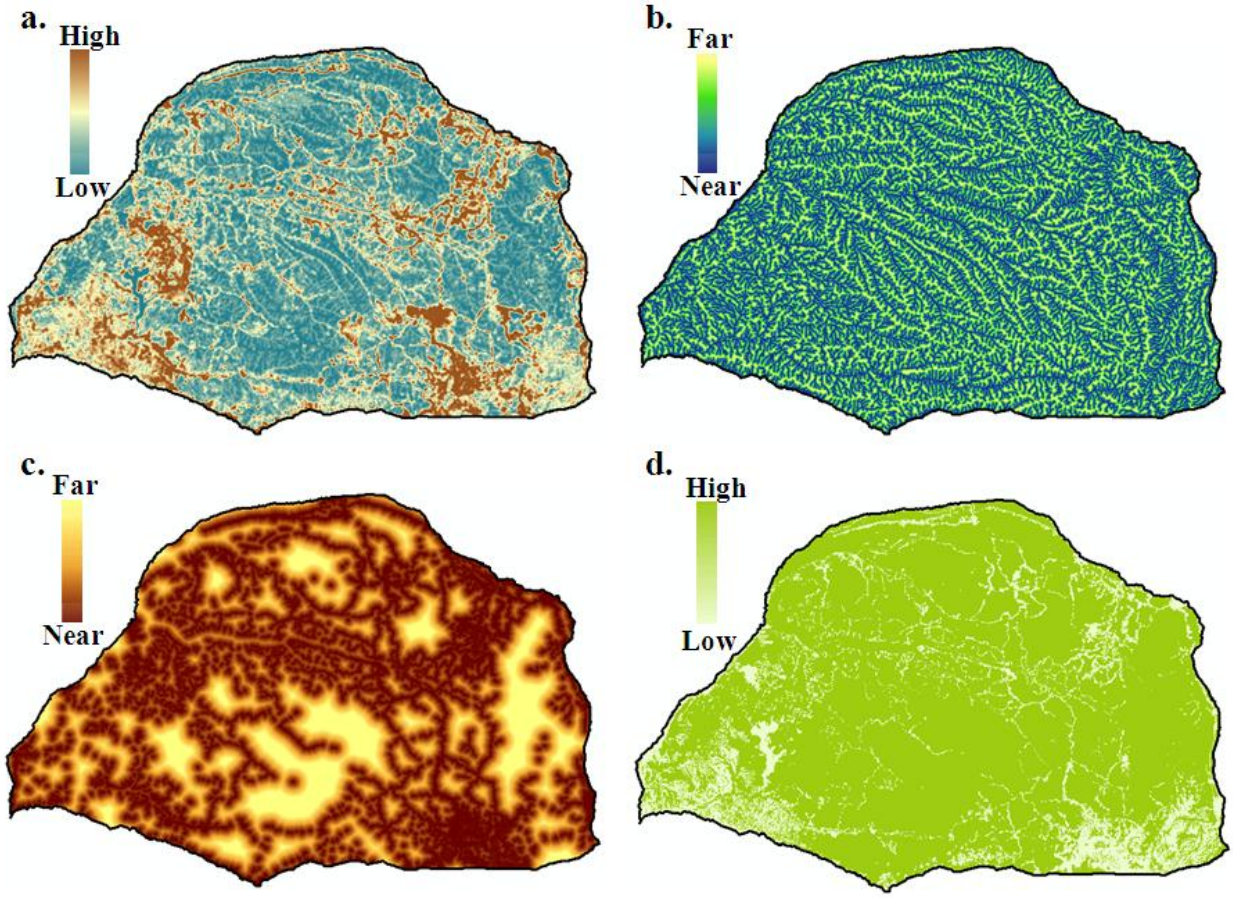

Figure 3.3. Maps of the selected environmental variables used in the final model to predict relative suitability of conditions for bonobos: a.) edge density (km/10km^2), b.) distance from river (km), c.) distance from agriculture (km), and d.) percent-forest landcover. All maps are drawn at 100-m resolution.

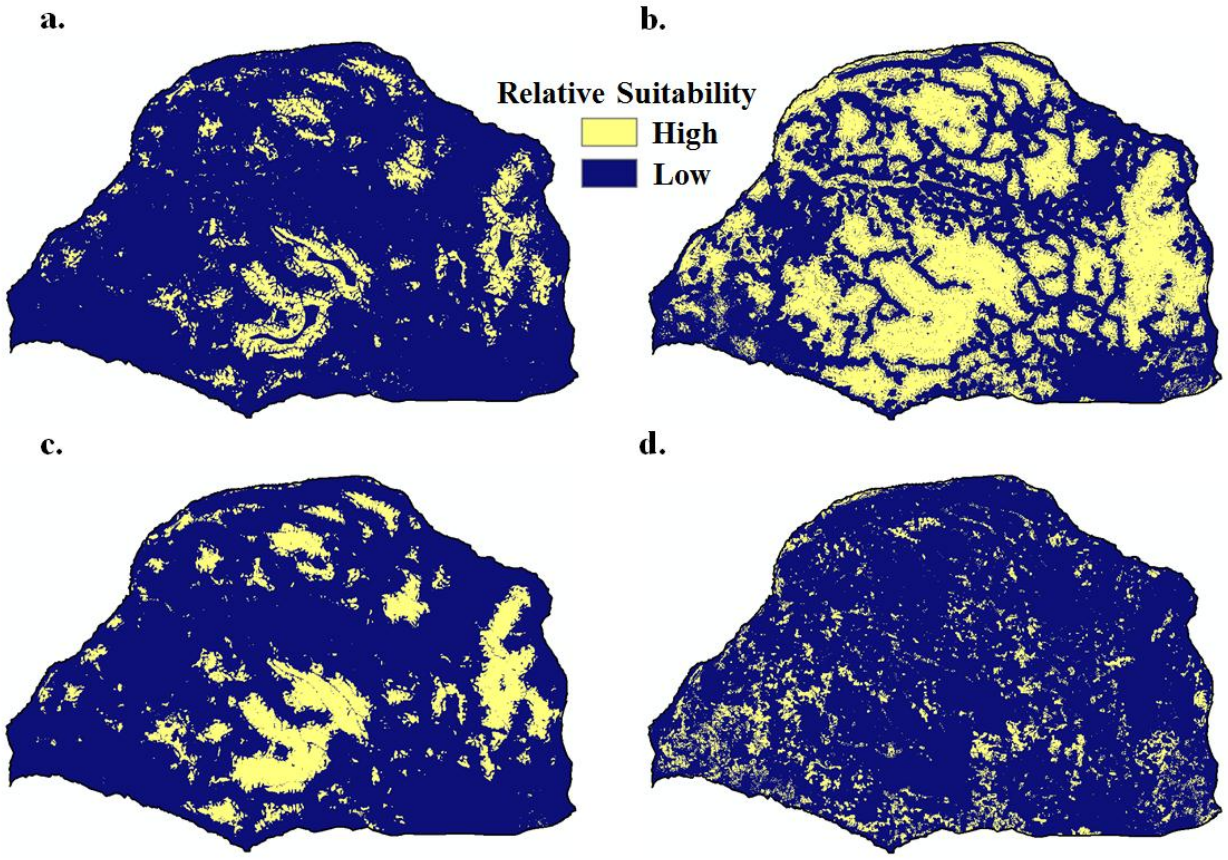

Figure 3.4. A comparison of suitable conditions for bonobos as predicted by 4 rangewide models differing in their presence-only input data. Each was built from nest-block data limited to the following corresponding regions a.) MLW-only, b.) TL2-only, c.) SNP-only, and d.) LT-only, Democratic Republic of Congo. Note the similarity between a, c, and the final model (Fig. 3.2).

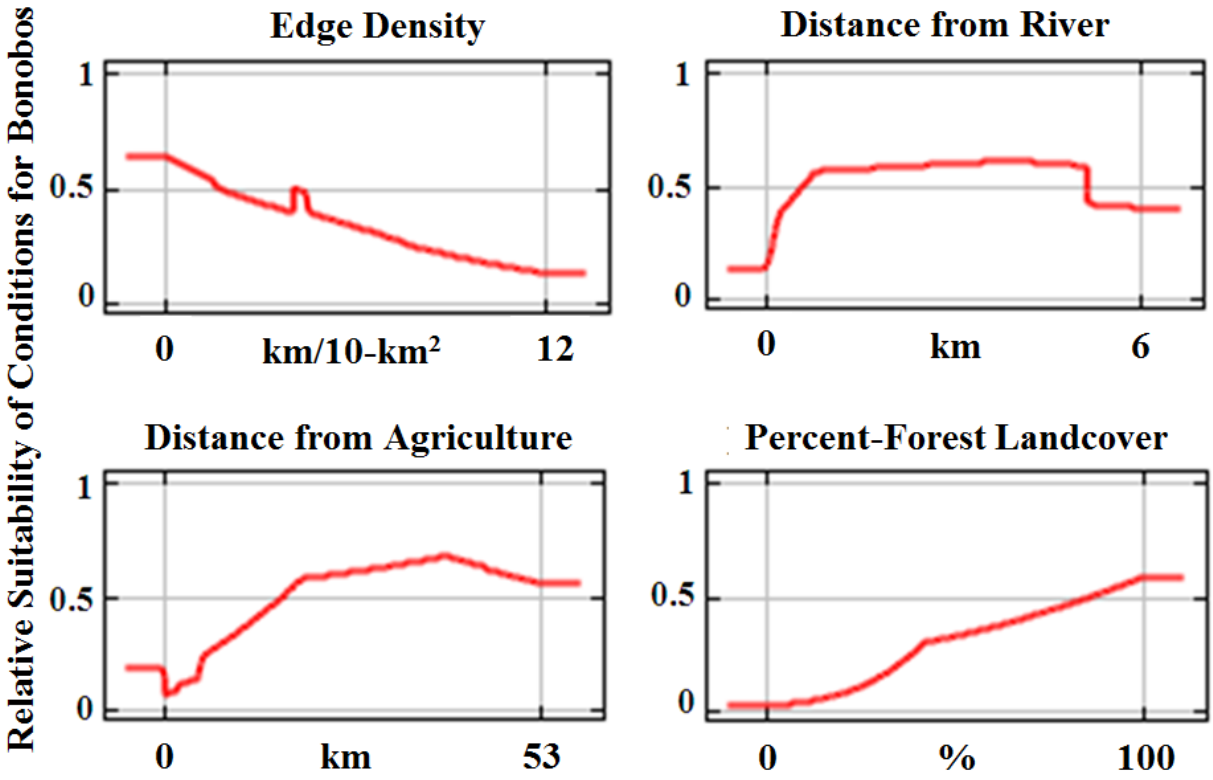

Figure 3.5. The response curves of relative suitability of conditions for bonobos and the predictor variables for the final rangewide MaxEnt model, depicting a negative relationship for forest fragmentation as measured by edge density (km/10km^2), and positive relationships for distance from river (km), distance from agriculture (km), and percent-forest landcover.

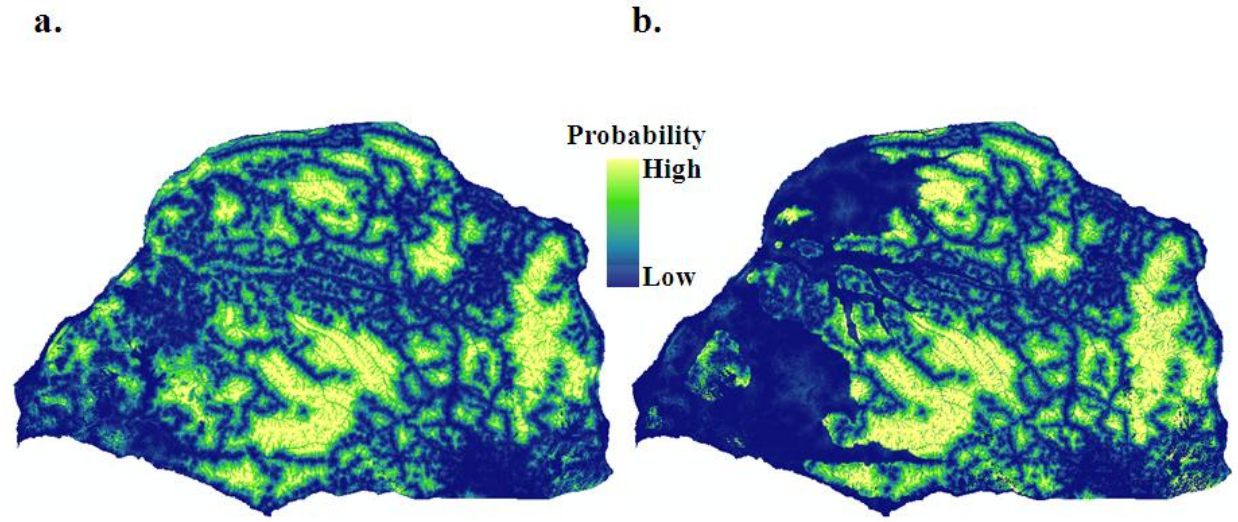

Figure 3.6. A comparison of the MaxEnt rangewide spatial predictions of relative suitability for bonobos a.) without elevation and b.) with elevation as a fifth variable, Democratic Republic of Congo.

CHAPTER 4

QUANTIFYING BONOBO (*PAN PANISCUS*) SITE OCCUPANCY: THE INFLUENCE OF LANDSCAPE AND LOCAL MEASURES OF HUNTING PRESSURE[3]

[3] Hickey, J.R., M.J. Conroy, C. Moore, and N.P. Nibbelink. 2012. To be submitted to *Biological Conservation.*

ABSTRACT

The use of classified data from satellite imagery to estimate species' distributions has become widespread and is often used for conservation planning purposes. Therefore, it is important to understand the relative strength of such classified data to predict species occurrence compared to field-derived data and to assess the conservation implications of both types of data. We quantified the effect of various remotely-derived versus field-derived predictor variables on the probability of site occupancy by bonobos (*Pan paniscus*). Bonobos are great apes endemic to the Democratic Republic of Congo (DRC) primarily inhabiting large tracts of lowland rainforest that are under pressure from timber harvest and land-use change. The IUCN^{TM} classifies bonobos as endangered and lists direct loss from illegal hunting and indirect losses from habitat degradation via forest fragmentation as the primary threats to bonobos. In 2009, we collected site occupancy data based on bonobo nest observations on 68 km of transect in the Maringa-Lopori-Wamba landscape, DRC. We analyzed double-independent observer data using mark-recapture techniques to estimate detection probabilities in order to calculate unbiased estimates of abundance and site occupancy. Using logistic regression, we evaluated bonobo site occupancy in relation to both landscape-scale measures of forest fragmentation and hunter accessibility as well as local measures of hunting pressure (e.g. number of machete cuts in the vegetation and number of traps per site). We demonstrated that the remotely-derived forest edge density metric [ED, (m/ha)], a measure of forest fragmentation, performed at least as well as the best-performing field-derived predictor (machete cuts). Using an information-theoretic approach, we found that ED appeared in all 13 of the best-performing models, whereas machete cuts appeared in 11 of 13. Assuming the other factors stayed constant, the odds of bonobo site occupancy were 1.27 times *lower* for each unit increase in ED. Similarly holding the other factors constant, bonobos were 1.27 times *less*

likely to occupy an area for each additional machete cut per site. Comparing areas similar in hunting pressure but different in forest fragmentation demonstrated significantly lower bonobo occupancy correlated with high fragmentation. By contrast, areas of differing hunting pressure yet with similarly intact forest exhibited significantly lower bonobo occupancy under high hunting pressure. Our results indicate that forest fragmentation and hunting both negatively influence bonobo occupancy, and suggest potential negative effects of forest fragmentation independent of hunting.

INTRODUCTION

The rapid conversion of land to meet human needs creates a conservation challenge, and emphasizes the need for relevant data to support conservation planning. Landscape-level variables derived from remote sensing can contribute to more informed decisions, yet need to be grounded in established relationships with the elements of biodiversity targeted for conservation. The difference in relative scale between measures of many landscape- versus local-level variables can cloud our understanding of the causal mechanism relating the two. For example, a substantive body of research has documented the empty forest syndrome – in which seemingly suitable stands of intact or relatively intact forest are devoid of most fauna. The mechanism causing empty forest syndrome has generally been attributed to local hunting (Redford 1992, Fa and Brown 2009, Wilkie *et al.* 2011). Wilkie *et al.* (1992) demonstrated that forest fragmentation via roads and transects from logging activities exacerbated hunting pressure on forest fauna in the Republic of Congo. Therefore, in the cases of fragmentation-induced empty forest syndrome, we (Chapters 2 and 3) hypothesized that remotely-sensed data measuring forest fragmentation and landscape-level proxies of hunter access (distance from agriculture, distance from road, distance from rivers) may correspond to relative hunting pressure for many hunted species because areas near

agriculture, roads and rivers are necessarily near areas of higher human concentration. However, it remains untested whether those landscape metrics actually relate to relative hunting pressure.

As a case in point, bonobos (*Pan paniscus*) are endangered great apes that are in jeopardy due to illegal hunting (poaching) and habitat fragmentation (Fruth *et al*. 2008). We (Chapter 3) demonstrated that habitat fragmentation as measured by edge density (ED) and relative hunter access as measured by distance from agriculture, distance from road, and distance from rivers effectively predicted rangewide occurrence of bonobo nest blocks. Yet, the pervasiveness of hunting throughout the bonobo's range – including areas that are legally protected (Dupain and Van Elsacker, 2001; Hart *et al.*, 2008) – precluded a rangewide assessment of the predictive importance of landscape-level factors in the absence of hunting (Chapter 3). The difficulty is that, at the rangewide scale, there are essentially no areas without hunting. Therefore, there is a need for fine-scale analyses in areas that differ in relative hunting pressure in order to compare the utility of both remotely-sensed and field-derived data in predicting bonobo occupancy and to assess the conservation implications of those factors. Over the long term, it will be important to clarify the mechanism by which landscape-level predictors relate to bonobo occupancy. Based on previous studies (Wilkie *et al.* 2011, Chapters 2 and 3 this document), the assumed causal mechanism is hunting.

We evaluated bonobo site occupancy within the Maringa-Lopori-Wamba (MLW) landscape in relation to both landscape-level predictors, as well as local evidence of human presence. We quantified and compared the influence of these factors on probability of bonobo site occupancy and suggest that this information can inform and focus bonobo conservation efforts. Additionally, we anticipated imperfect detection of bonobo nests directly seen on the transect line, violating a key assumption of density estimation via distance sampling (Buckland *et al.* 2001).

Thus, we employed double-independent observer techniques (Williams *et al.* 2002) to estimate detection probability and to correct estimates or abundance and occupancy accordingly. Given that humans in this landscape must hunt, farm, and harvest trees to shape their livelihoods, this project seeks to provide data that decision makers can use to optimally zone sylvo-agro-pastoral (Dupain *et al.* 2009) activities and protected areas in order to ensure the persistence of bonobos. In addition, these results provide a baseline for long-term studies striving to elucidate causal mechanisms relating bonobo occupancy to remotely-derived data.

METHODS

Study Area

MLW (Figure 4.1) is an area designated as a conservation landscape by the Central African Regional Program for the Environment (CARPE), a branch of the U.S. Agency for International Development (USAID) (Hickey and Sidle 2006). MLW was selected as a CARPE landscape specifically for the conservation of bonobos in conjunction with alleviation of poverty (Hickey and Sidle 2006). MLW is approximately 74,000 km^2 and characterized by large areas of intact lowland rainforest, human settlement, slash-and-burn agriculture, and numerous large timber concessions (totaling >6,000 km^2) in different states of harvest rotation or harvest planning (Dupain *et al.* 2009). We conducted our field research both inside and outside of a recently designated protected area known as the Lomako-Yokokala Faunal Reserve (LYFR) and a logged area near the town of Kee, DRC (Figure 4.1).

Field Data Collection

From February to July 2009, we surveyed 68 km of line-transects and recorded locations of all detected bonobo nests and human signs (machete cuts, traps, hunting camps, paths, roads, and log-cut trees). We used double independent-observer search methods (Williams *et al.* 2002)

thereby surveying all transects twice in order to quantify and address detection probability, which is critical for unbiased estimates of occupancy with imperfect detection (MacKenzie *et al.* 2006). We conducted transects in four major regions stratified by forest fragmentation as measured by ED (m/ha) (see GIS Methods). They ranked from lowest to highest ED as follows: (1) Lomako South, inside the southern portion of LYFR, (2) Lomako North, inside the northern portion of LYFR, (3) Mawa, an unlogged region west of Lomako South, and (4) Kee, a logged area northwest of LYFR (Figure 4.1). All regions differed significantly in ED (Figure 4.2) except the two Lomako regions which shared similarly low ED (intact forest). We further stratified random start and end points of all transects *a priori* in ArcGIS 9.3 (ESRI, Redlands) using "distance from fire" (see GIS Methods), a measure expected to correlate with proximity of human presence. We found that fire points corresponded more accurately to the locations of roads, villages and slash-and-burn agriculture than the available layer on human settlements. In this landscape, all communities practice slash-and-burn agriculture creating fires sufficiently large that satellites detect them. In stratifying by distance from fire, we attempted to capture site occupancy data along a gradient of potential human threat in every region with strata further from fire expected to experience lower likelihood of hunting pressure.

GIS Methods

We applied reported nest-group distances and the raster pixel size to define bonobo sites. When assigning nests to nest groups, the suggested cutoff distance between nests within a single nest group is 30 m (Mulavwa *et al.* 2010). Our raster pixels were 57-m x 57-m, consequently sites for this study are 120-m long and correspond approximately to pixel length plus 30-m buffer on either side. In ArcGIS 9.3, we separated the surveyed transects into 542 sites. For each site, we

summed the total count of bonobo nests and each human sign (machete cuts, traps, hunting camps, log-cut trees, paths, and roads).

Our objective was to evaluate the relative magnitude of effect from landscape variables developed from remote sensing data versus the local counts from field surveys described above. Therefore, we created three metrics thought to represent habitat fragmentation, relative hunting pressure, or both. We defined forest ED as the linear edge between forest and non-forest in a given area and used ED as a measure of habitat fragmentation. ED was shown to be a strong predictor of bonobo nest occurrence in MLW and rangewide (Chapters 2 and 3); specific methods for calculating ED may be found in Chapter 2. Since ED captured the fragmentation from rivers, roads, timber harvest, and agriculture it not only related to habitat degradation, but also to potential hunter access via any or all of these human created or natural access routes (Laurance *et al.* 2009). In addition, we developed specific GIS layers for distance from river and distance from fire as additional proxies for relative hunting pressure due to ease of hunter access. In MLW, rivers are the primary travel corridors, hence areas closer to rivers are also closer to potential hunter access. Fire points were detected via LANDSAT imagery and then interpreted and provided by the University of Maryland (Davies *et al.* 2009). The fire-points database included a rating of relative confidence (0-100%) in the accuracy of its classification as a fire. Based on guidance in the associated metadata, we used fire points rated $\geq$ 50% confidence in determining distance-from-fire strata for our study design. However, during the field season we noted that even low confidence fire points tended to be actual slash-and-burn fields, therefore the distance-from-fire predictor variable includes fire points of all confidence levels in lieu of spatial data on village locations. We calculated the Euclidean distance from fire points (Davies *et al.* 2009) and

rivers (USGS 2000), thereby creating two raster data layers from which to extract values of each covariate to our sites.

Population estimation, detection probability, and occupancy estimation methods

Viewed from the forest floor, fresh bonobo nests are large green leafy clusters occurring at various heights amid equally green foliage of the forest canopy. Lack of dramatic color or texture contrast and potential for vegetation to obstruct viewing can cause some nests to go undetected; thus nondetection cannot be equated to nonoccurrence. Therefore, we analyzed individual nest mark-recapture histories with Huggins closed capture population estimation models (Huggins 1989) in Program MARK (version 6.1). This allowed us to provide unbiased estimates of *N*, the number of nests along the transects and to assess potential heterogeneity in detection probability (*p*) based on observer (Team A or B) and time (survey occasion 1 or 2). Following Mohneke and Fruth (2008), we estimated density of bonobo nests using the following formulas:

$$\hat{D}_1 = \frac{n}{dr \times pr \times L \times 2w} \qquad (1)$$

and

$$\hat{D}_2 = \frac{\hat{N}}{dr \times pr \times L \times 2w} \qquad (2)$$

thereby incorporating the estimated number of nests (either the naïve count of *n* detections or the unbiased estimate of nests $\hat{N}$ from Program MARK), nest decomposition rate (*dr*), nest production rate (*pr*), total length of the transects surveyed (*L*), and approximate mean viewing distance along either side of the transects ($2w$). To develop a range of estimates for *D*, we applied two different estimates of *dr*, 99 d and 75.5 d (Eriksson 1999 in Mohneke and Fruth 2008, and Mohneke and Fruth 2008, respectively) and *pr*, 1.37 and 1 (Mohneke and Fruth 2008 and Reinartz *et al*. 2006, respectively). To determine *w*, we measured perpendicular distance to

detected nests along 13 km of transect and selected the distance at which frequency of observations declined sharply.

For unbiased estimates of occupancy, we built a series of models (MacKenzie *et al.* 2006) in Program MARK, estimated the probability of site occupancy (ψ) and *p*, and examined the effect of environmental predictors on occupancy. This procedure computes the probability of site occupancy using repeated site visits in a closed population to estimate *p* and uses that value to estimate the combined probabilities that a given site is either: 1) occupied and detected, 2) occupied but not detected, and 3) not occupied. In addition, we looked for evidence of site-level heterogeneity in *p* using mixture models. A fourth option is detecting the target in error when it is actually absent (such as erroneously recording a cluster of lianas as a nest). We believe the latter is unlikely because of the distinctive construction of bonobo nests that often includes intertwined live branches. Prior to analysis we standardized all predictor variables by subtracting their mean and dividing by their standard deviation. Despite this procedure, adding environmental covariates in a given model caused unreliable results in Program MARK (e.g. estimates of 0 variance), therefore we re-ran the univariate and multivariate models in WinBUGS (version 1.4.3) using Bayesian analysis.

WinBUGS provided the posterior distribution of ψ from the product of the likelihood of the model (given the data) and prior distributions of model parameters using a Gibbs sampler (Link *et al.* 2002). For each model, we employed a uniform distribution between 0 and 1 for the prior of *p,* and normal distributions with mean=0 and precision=0.37 for the priors of all logit-linear coefficients. We initialized each of three chains with *p* values of 0.3, 0.5, and 0.7 and coefficient values of -1, 0, and 1, respectively, and ran them for 103,000 iterations each then deleted the first 3,000 iterations as burn in. Although Bayes analysis provided consistent estimates

of p and ψ across all models, we were unsuccessful in modeling potential relationships between ψ and the environmental covariates using occupancy modeling in either a Bayesian (WinBUGS) or likelihood (Program MARK) approach. Although these procedures normally accommodate zero-inflated data, our data likely were limited by an exceptionally high number of zeros (473 of 542 sites were unoccupied) and would have benefitted from >2 occasion histories/site or more sites surveyed. Therefore, we used logistic regression models and an information-theoretic approach (Burnham & Anderson 2002) to evaluate the influence of environmental predictor variables on occupancy.

Logistic regression and multi-model inference

We ranked all Program MARK, WinBUGS, and logistic regression models (Program R) using an information-theoretic (AIC) approach to model selection discussed in Akaike (1973) and Anderson *et al*. (2000). Under each modeling framework, we developed a candidate set of models describing potential relationships between site occupancy and unstandardized landscape and local variables (Table 4.1). Information-theoretic methods (Anderson *et al*. 2000) evaluate the relative plausibility of different models using estimates of likelihood. To reduce the potential for over-fitting, we examined the parameter estimates of univariate models for nine predictors and retained those exhibiting potential significance at $\alpha \leq 0.1$ for use in a global logistic regression model (Millington *et al.* 2010). In order to avoid multicollinearity, we calculated Pearson's correlation coefficient, *r*, on all pairs of predictors and eliminated the weaker predictor of any two correlated ($r>0.49$) variables from the global model. We built a set of candidate models to predict site occupancy from all possible combinations of non-correlated parameters contained in the global model. We calculated Akaike's Information Criteria (AIC; Akaike 1973) with the small-sample bias adjustment (AICc; Hurvich and Tsai 1989) to evaluate the fit of each candidate model. Then

to compare models, we assessed the relative fit of each candidate model by calculating Akaike weights (Anderson *et al*. 2000), with the best-fitting candidate model having the greatest Akaike weight. We created a confidence set of models that included only those candidate models with Akaike weights greater than 10% of the largest Akaike weight as suggested by Royall (1997). We considered models with Akaike weights less than 10% of the greatest weight to have too little evidence to be plausible explanations for bonobo site occupancy.

The above estimates, predictions, and associated confidence intervals are conditional on given models, and do not reflect uncertainty about model identity. Therefore, following Burnham and Anderson (2002), we estimated model-averaged coefficients and unconditional standard errors in order to incorporate model uncertainty. We weighted parameter estimates and corresponding standard errors from each candidate model by that model's associated Akaike weight and summed across the different models to develop a composite model. We decided *a priori* to include all parameters found in the confidence set of models in our final composite model and based all inferences on the composite model.

In logistic regression predictions are expressed in log-odds, and odds ratios are used to interpret the relative strength of factors affecting the response assuming the other factors are held constant. In order to calculate an odds ratio, the parameter estimate for each coefficient must be back-transformed with the exponential function, e^x, where x is the logit-linear parameter estimate. This procedure allows inference of the relationship between the predictor and response variables (Hosmer and Lemeshow 1989). We then calculated the odds ratio for each predictor in the composite model in order to infer the direction and magnitude of the relationships with bonobo site occupancy. Odds ratios >1 indicate positive relationships, such that with each unit increase in the variable, the probability of occupancy is e^x times greater. Odds ratios <1 indicate a negative

relationship and are interpreted more easily by taking the inverse and stating "sites are $1/e^x$ times" *less* likely to be occupied with each unit increase in the parameter.

ANOVA corrected for multiple comparisons

We used one-way ANOVAs to test whether there were differences among regions with respect to each variable (machete cuts, traps, roads, ED, distance from fire, and distance from river), applying the Tukey correction for multiple comparisons. Results were then compared to bonobo occupancy in each of the regions to help explain the pattern of occupancy relative to regional conditions.

RESULTS

Field Surveys, detection probability, and occupancy estimation

We detected a total of 338 nests of which 319 were usable for this analysis, the others being opportunistically sighted during hikes to or from transects. We found no nests in Kee, the previously logged region, and we detected none in Lomako North. The latter is an area where abundant hunting signs (fresh, set traps) were found, despite its official designation as a protected area (Figure 4.2). Examined in Program MARK, occasion histories per individual nest resulted in stable models and estimates of p and $\hat{N}$. Huggins closed-capture population estimation calculated $\hat{N}$ (±SD) as 352.7 (±12.98). Using the naïve count for number of nests, n=319 and an effective strip width $2w$=0.06 km, then the density of nest-building bonobos from equation (1) equals:

$$\hat{D}_1 = \frac{319}{99 \times 1.37 \times 68 \times 0.06} = 0.576 \text{ bonobos/km}^2.$$

Whereas holding all other estimates constant and employing the number of nests corrected for p, $\hat{N} = 353$, the $\hat{D}$ from equation (2) equals:

$$\hat{D}_2 = \frac{353}{99 \times 1.37 \times 68 \times 0.06} = 0.638 \text{ bonobos/km}^2.$$

Because the values of *dr* and *pr* can vary by location and season we calculated a range of estimates for $\hat{D}_1$ and $\hat{D}_2$ (Table 4.2).

We found individual nest-detection probability varied significantly by observer but not by survey occasion. Mean detection rates of Teams A and B were 0.78 and 0.58, respectively. Within Team A, detection rate for occasion 1 was 0.83 (±0.04) and for occasion 2 was 0.73 (±0.04) and did not differ significantly (*t*-statistic=1.72, d.f.=317, *P*=0.09). Within Team B, detection rate for occasion 1 was 0.63 (±0.06) and for occasion 2 was 0.52 (±0.05), also not differing (*t*-statistic=1.32, d.f.=317, *P*=0.19). Teams A and B differed significantly from each other during occasion 1 (*t*-statistic=2.43, d.f.=317, *P*=0.016) and occasion 2 (*t*-statistic=3.46, d.f.=317, *P*<0.001). The difference in observer detection rates was homogenized over occasion histories, because the survey protocol included periodically alternating Team A and B between occasion times 1 and 2. Mixture models for *p* using site occasion histories were not supported as all mixture models caused implausible results in Program MARK (e.g. estimates of 0 variance). Assuming a constant *p,* the Program MARK estimate and the mean of the posterior distribution derived from Bayesian analysis shared similar values for *p* (±SD) of 0.745 (±0.047) and 0.737 (±0.047), respectively.

Modeling a constant *p* and ψ, the Program MARK estimate and the mean of the posterior distribution derived from Bayesian analysis concurred with ψ (±SD) of 0.136 (±0.016) and 0.138 (±0.016), respectively. We determined the minimum convex polygon (MCP) around surveyed transects (Figure 4.3) which encompasses 3,115 km^2, 79% of which falls within the protection of the LYFR. Extrapolating the mean of the ψ values to the MCP gives:

$$3{,}115\ km^2 \times 0.137 = 426.8\ km^2$$

occupied within the MCP. Inverting the occupancy estimate, we can see that at any given time approximately (1- 0.137)×100 = 86.3% of the MCP is *un*occupied by bonobos, despite being predominantly protected lowland rainforest.

While both approaches produced stable models with similar estimates when covariates were excluded, adding covariates to the models produced unrealistic estimates of ψ (e.g. lower than observed) in Program MARK, whereas in WinBUGS the null model ranked the highest based on Akaike weight. Due to these uninformative results we used logistic regression to evaluate the influence of covariates.

Logistic regression

We collapsed occupancy histories into presence-absence data combining data from both occasions 1 and 2 in order to conduct logistic regression. This procedure increases the power of the data to detect a pattern with the covariates, however it also eliminates consideration of detection probability (p). Yet, we reason most occupied sites were detected with our protocol. Since p is the probability of detecting a nest, given it is there, the probability of *not* detecting a nest given it is there is $(1-p)$. In general, non-detection at a site that contains at least one nest (false absence) can be estimated by $(1-p)^i$, where i is the number of survey occasions. In this case, the best-ranked occupancy model had constant p between occasions and mixtures were not supported, therefore we estimated the probability of false absences as:

$$(1-\bar{p})^2 = (1-0.74)^2 = 0.068,$$

where $\bar{p}$ was the mean of Program MARK and Bayesian analysis estimates for site-level detection probability. The corresponding probability that we correctly determined site occupancy was $1-0.068=0.932$. Based on this high probability of correct site classification, relatively few

occupied sites went undetected, therefore we analysed the effect of predictors on presence-absence using logistic regression.

In Program R, we constructed a global model with 6 of 9 possible predictors. There was no evidence of multicollinearity (all Pearson's $|r|<0.44$); however we excluded hunting camps due to low occurrence (n=7), log-cut trees due to abnormal behavior caused by zero variance at occupied sites (100% of occupied sites had zero log-cut trees within 100 m), and paths due to non-significance in the univariate model (P=0.9). Out of 64 models, 13 had Akaike weights ≥ 10% of the best model and so were included in the final composite model (Table 4.3). ED was the most prevalent parameter, being present in all models in the confidence set. Machete cuts occurred in 11 and distance from river occurred in 10 of the top 13 models. Together, ED, distance from river, and machete cuts were the most important predictors of site occupancy. As expected, sites were less likely to be occupied with increasing ED and machete cuts, whereas sites were more likely to be occupied with increasing distance from rivers (Table 4.4).

Back-transforming the parameter estimate of ED produced the odds ratio $e^{-0.2393} = 0.787$; and because 0.787 is <1 the odds ratio indicates a negative relationship between ED and site occupancy. Therefore, the odds of bonobos occupying a site were (1/0.787)=1.27 times *lower* for each additional m/ha (or scaled to the approximate size of a bonobo's homerange: 1.27 times *less* for each 2-km increase of edge in the surrounding 20 km^2) (Table 4.4). Similarly, sites were 1.27 times *less* likely to be occupied for each additional machete cut within a 120-m site. Sites were 1.47 times *more* likely to be occupied for each 1-km increase in distance away from river, yet its lower 90% CI approximated 0 thereby demonstrating a weaker effect for distance from river than for either ED or machete cuts. All other parameters had 90% confidence intervals that fully

encompassed 0, indicating inconclusive results because we could not determine the direction (positive or negative) of the relationships.

ANOVA analysis

One-way ANOVAs showed differences in landscape-scale and local-scale variables among sample regions. Overlaying bonobo occupancy allowed us to tease out potential differences due to hunting versus habitat structure alone (Figure 4.2). For instance, Lomako North is within an officially designated protected area, with low mean (±SD) ED 1.74 (±1.6) m/ha that was significantly farther from fires than the other regions (mean (±SD) fire distance 20.08 (±1.41) km, F=196.24, d.f. 3, 538, P<0.0001 for all comparisons). Despite these qualities, Lomako North had zero detected nests and very high numbers of machete cuts and traps, many of which still had animals captured in them. Lomako North and the logging area, Kee, did not differ significantly in mean number of machete cuts per site and these two regions had significantly more machete cuts than either Lomako South or Mawa (Figure 4.2a). Lomako North and Kee, both of which had zero bonobo nests detected, had significantly more traps than Lomako South (Figure 4.2b). In fact, Lomako North had significantly more traps than all other regions. Lomako North and Lomako South were the most similar in terms of mean ED (Figure 4.2d); however, these two regions were the most dissimilar in mean number of traps per site (F=20.00, d.f. 3, 538, P<0.0001) (Figure 4.2b).

Comparing the bonobo-occupied regions of Lomako South and Mawa to the unoccupied logged region of Kee indicated that neither of the former regions differed significantly in mean number of traps from Kee. While not a significant difference, Mawa actually had a higher mean number (±SD) of traps per site than Kee, 0.63 (±1.06) and 0.44 (±0.86), respectively. The

attribute that did differ between Kee and the two bonobo-occupied regions was ED (Figure 4.2d), with Kee exhibiting significantly greater ED (F=633.03, d.f. 3, 538, P<0.0001).

Interestingly, the two bonobo-occupied sites, Lomako South and Mawa differed significantly in mean number (±SD) of traps per site, 0.19 (±1.32) and 0.63 (±1.06), respectively (Figure 4.2b). Lomako South exhibited the fewest traps of all the regions and the highest site occupancy by bonobos.

DISCUSSION

We estimated overall bonobo density and site occupancy within the minimum convex polygon around our transects, and quantified important influences of hunting pressure on bonobo occupancy from both remotely-sensed and field-derived data. Our survey design incorporated gradients of potential human threat which resulted in occupancy samples that included forest unoccupied by bonobos, thereby avoiding inflated estimates of occupancy. In addition, we demonstrated that line-transect bonobo nest surveys involve imperfect detection (including at 0-m distance from the transect where traditional distance-methods assume p=1) and adjusted estimates of nest counts accordingly. An information-theoretic approach to model selection identified that habitat fragmentation (ED), number of machete cuts, and distance from rivers were the most important predictors of those evaluated. Regional comparisons revealed the importance of hunting in the absence of fragmentation and the importance of fragmentation when hunting pressure is similar.

This study generally supported estimates of bonobo density generated by studies employing distance methods (Buckland *et al.* 2001). Using two different nest-decomposition rates and nest-production rates from the literature, we computed four estimates of detection-corrected bonobo density, D, ranging from 0.638-1.15 bonobos/km^2 all of which fell within the range of

values reported in estimates for MLW (0.28 bonobos/km^2 to 1.4 weaned bonobos/km^2, Hashimoto and Furuichi 2001 and Eriksson 1999, respectively).

Just as it is important to sample areas of both low and high bonobo occupancy in order to avoid correspondingly inflated or deflated density estimates, we believe it is also important to appropriately incorporate detection probability, *p*, in sample design to avoid biased estimates of occupancy, abundance, and density. Traditional distance-sampling techniques for estimating density incorporate functions for declining *p* based on increasing distance from the transect, but assume perfect detection at 0-m distance from the transect. We offer an alternate survey approach that addresses imperfect detection at 0-m from the transect. Our estimate of $\hat{p}$=0.74 based on mark-recapture analysis of nests provides a reference point for comparisons to future estimates by other teams of observers.

Comparisons between regions underscore the importance of both local-scale and landscape-scale predictors. Consider Lomako North, a region that contained no detected nests despite having apparent outward characteristics of favorable habitat including low fragmentation and large distance from fire. Based on these landscape characteristics, we might have expected bonobo occupancy to be high, or at least detected. Instead, this area had zero detected nests and significantly higher numbers of traps than any other region. For Lomako North, number of traps was the prevailing attribute correlated with the observed low occupancy by bonobos. These results substantiate previous reports that hunting is a major problem even in intact forest (Redford 1992, Hart *et al.* 2008, Wilkie *et al.* 2011), and can lead to the empty forest syndrome in which a forest appears otherwise suitable yet is depauperate of fauna.

Results from Lomako North demonstrate that bonobos inhabiting a nationally designated protected area are not necessarily effectively protected *per se*, and that extensive improvements

are needed in law enforcement as well as in proactive efforts to provide alternatives to local peoples. For this site specifically, we recommend additional financial and capacity-building support for a guard station located on the Yokokala River in the Ekombe territory. We envision such a station employing and training locals as guards, thereby contributing to increased employment opportunities. We expect that regular patrols of the northeastern quadrant of LYFR as well as inspections of boats commuting on the Yokokala River would decrease hunting pressure in this portion of the Reserve. We assume that since important drains on wildlife populations come from non-local commercial hunters (Hart *et al.* 2008, Fa and Brown 2009), finding and confiscating bushmeat derived from protected areas is an essential element to reducing the problem of poaching.

Because fragmentation can increase hunter access to forest areas, it can be difficult to demonstrate whether the negative effect of fragmentation on bonobo occupancy is due to habitat preference or confounded by hunting pressure. This study provides one example supporting fragmentation effects under apparently low hunting pressure. In the case of the logged area compared to the two bonobo-occupied regions, the logged area differed significantly in fragmentation (ED) but not in mean number of traps. Because the logged area had similar hunting pressure, but high ED and zero nests detected, we concluded that fragmentation is important to consider for bonobo distributions regardless of hunting pressure. Conversely, Lomako North and Lomako South did not differ significantly in ED, yet Lomako North had significantly more traps. Having detected zero nests in Lomako North, we concluded that hunting is an important variable to consider for bonobo distributions regardless of fragmentation. Essentially, both landscape- and local-level variables are important in shaping bonobo distributions, and both are important to consider in landscape management in order to protect this species.

A weakness in this study is that we do not have nest- or trap-occurrence data prior to the logging event, hence our study represents a snapshot in time. For example, based on our data alone, we cannot know whether Kee had higher bonobo occupancy prior to logging. If it did, we cannot discern from our single-season data whether Kee was hunted and drained of bonobos (perhaps during or immediately after logging), or if bonobos have extremely low occupancy there now because of the high ED itself. For this reason, we advocate long-term repeated studies in these and other regions in order to build datasets that can detect factors related both to empty forests as well as factors contributing to high bonobo occupancy. This study highlights the importance of both forest fragmentation and indirect measures of hunting pressure as factors influencing bonobo occupancy and quantifies the effects of each of these variables on probability of bonobo occupancy.

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Table 4.1. Remotely-sensed and field-derived data used in logistic regression models to predict the probability of bonobo site occupancy in the Maringa-Lopori-Wamba landscape, Democratic Republic of Congo.

Source	Predictor Variable	Units	Measure of	Expected relationship with bonobo occupancy
Remotely-sensed (Hickey *et al.* 2012, Hansen *et al.* 2008)	Edge Density	m/ha ($km/10km^2$)	Forest fragmentation	-
Remotely-sensed (Davies *et al.* 2009)	Distance from fire	km	Proximity to human settlements and, potentially, relative hunting pressure	+
Remotely-sensed (USGS 2000)	Distance from river	km	Proximity to human travel corridors	+
Field-collected	Machete cuts	Count/site	Human activity in forest	-
Field-collected	Traps	Count/site	Hunting activity in forest	-
Field-collected	Hunting camps	Count/site	Hunting activity in forest	-
Field-collected	Log-cut trees	Count/site	Human alteration of forest and potentially increased human access via log-extraction trails	-
Field-collected	Paths	Number of intersections /site	Human access	-
Field-collected	Roads	Number of intersections /site	Human access	-

Table 4.2. A range of naïve and detection-adjusted density estimates ($\hat{D}$, bonobos/km^2) based on bonobo nest surveys conducted during 2009 in the Maringa-Lopori-Wamba landscape, Democratic Republic of Congo using alternate estimates of number of nests (n and $\hat{N}$), nest-decomposition rates (dr),and nest production rates (pr).

		$\hat{D}_1$ (naïve)	$\hat{D}_2$ (adjusted for detection probability)
		n	$\hat{N}$
pr_1	dr_1 (99 d)	0.576	0.638
	dr_2 (75.5 d)	0.756	0.837
pr_2	dr_1 (99 d)	0.790	0.874
	dr_2 (75.5 d)	1.04	1.15

n = 319 naive (raw) nest count
$\hat{N}$ = 353 number of nests adjusted for detection probability
dr_1 from Eriksson (1999)
dr_2 from Mohneke and Fruth (2008)
pr_1=1.37 nests built per bonobo/d; from Mohneke and Fruth (2008)
pr_2=1 nest built per bonobo/d; from Reinartz *et al.* (2006)

Table 4.3. Model rank, predictor variables, number of parameters (*K*), AICc, ΔAICc, Akaike weights (*w*) for each model (*i*) in the confidence set of models predicting bonobo site occupancy in the Maringa-Lopori-Wamba landscape, Democratic Republic of Congo. Akaike weights are interpreted as the relative plausibility of candidate models.

Rank	Candidate Model	*K*	AICc	ΔAICc	w_i	% Max. w_i
1	ED+FIRE+RIVER+CUT	5	345.692	0.0000	0.1926	100.0
2	ED+RIVER+CUT	4	346.26	0.5678	0.1450	75.3
3	ED+RIVER+CUT+TRAP	5	346.907	1.2148	0.1049	54.5
4	ED+FIRE+RIVER+CUT+TRAP	6	347.008	1.3157	0.0998	51.8
5	ED+FIRE+RIVER+CUT+ROAD	6	347.732	2.0396	0.0695	36.1
6	ED+CUT	3	348.009	2.3168	0.0605	31.4
7	ED+RIVER+CUT+ROAD	5	348.294	2.6020	0.0524	27.2
8	ED+RIVER+CUT+TRAP+ROAD	6	348.947	3.2543	0.0378	19.6
9	ED+FIRE+RIVER+CUT+TRAP	7	349.053	3.3606	0.0359	18.6
10	ED+CUT+TRAP	4	349.506	3.8138	0.0286	14.9
11	ED+FIRE+RIVER+TRAP	5	349.639	3.9464	0.0268	13.9
12	ED+FIRE+CUT	4	349.817	4.1244	0.0245	12.7
13	ED+FIRE+RIVER	4	349.819	4.1272	0.0245	12.7

ED=edge density (m/ha); CUT=number of machete cuts; FIRE=distance from fire (km); RIVER=distance from river (km); ROAD=number of road crossings; TRAP=number of traps

Table 4.4. Model averaged parameter estimates, SE, 90% confidence intervals and odds ratios for the composite model predicting bonobo site occupancy in the Marina-Lopori-Wamba landscape, Democratic Republic of Congo.

	Number of Models Parameter Occurs In	Parameter Estimate	SE	90% CI Lower	90% CI Upper	odds[1] ratio	90% CI Lower	90% CI Upper	Interpretation[2] For each unit increase odds are
(Intercept)	13	-1.739	0.577	-2.69	-0.79	0.176	0.07	0.45	
ED (m/ha)	13	-0.239	0.049	-0.32	-0.16	0.787	0.73	0.85	1.27 times lower
CUTS	11	-0.235	0.120	-0.43	-0.04	0.791	0.65	0.96	1.27 times lower
RIVER (km)	10	0.384	0.235	0.00	0.77	1.468	1.00	2.16	1.47 times greater
FIRE (km)	7	-0.027	0.036	-0.09	0.03	0.973	0.92	1.03	1.03 times lower
TRAPS	6	-0.068	0.125	-0.27	0.14	0.934	0.76	1.15	1.07 times lower
ROADS	4	-0.012	0.176	-0.30	0.28	0.988	0.74	1.32	1.01 times lower

[1]Back-transforming the parameter estimate of ED produced the odds ratio $e^{-0.2393} = 0.787$; and because 0.787 is <1 the odds ratio indicates a negative relationship between ED and site occupancy.

[2]Therefore, sites were (1/0.787)=1.27 times *less* likely to be occupied for each additional m/ha (or scaled to the approximate size of a bonobo homerange: 1.27 times *less* likely to be occupied for each 2-km increase of edge in the surrounding 20 km^2).

ED=Edge density (m/ha); CUTS=Number of machete cuts; RIVER=Distance from river (km); FIRE=Distance from fire (km); TRAPS=Number of traps; ROADS=Number of road crossings

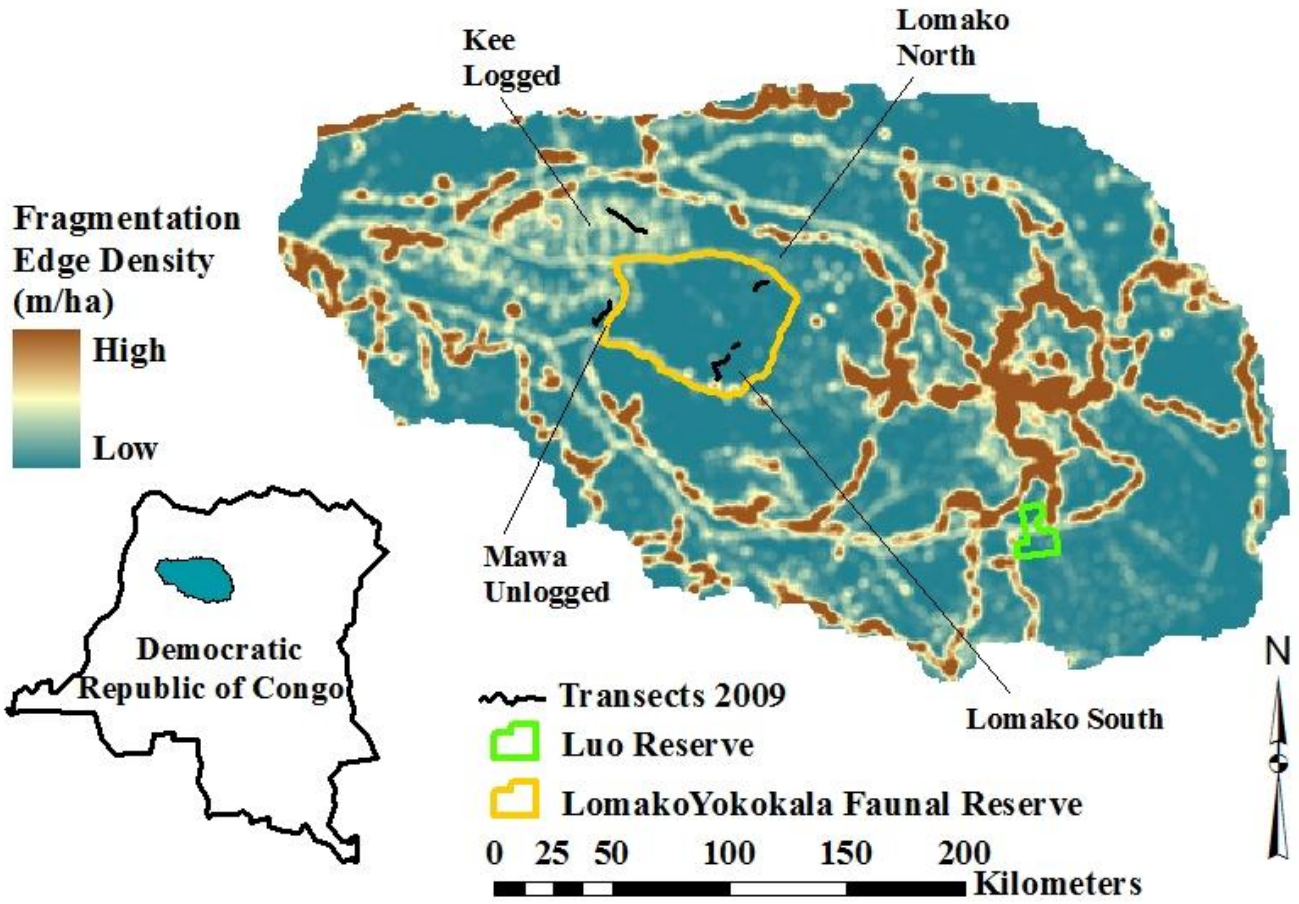

Figure 4.1. Four study regions (Lomako North, Lomako South, Mawa, and Kee), survey transects, protected areas, and edge density in the Maringa-Lopori-Wamba landscape, Democratic Republic of Congo.

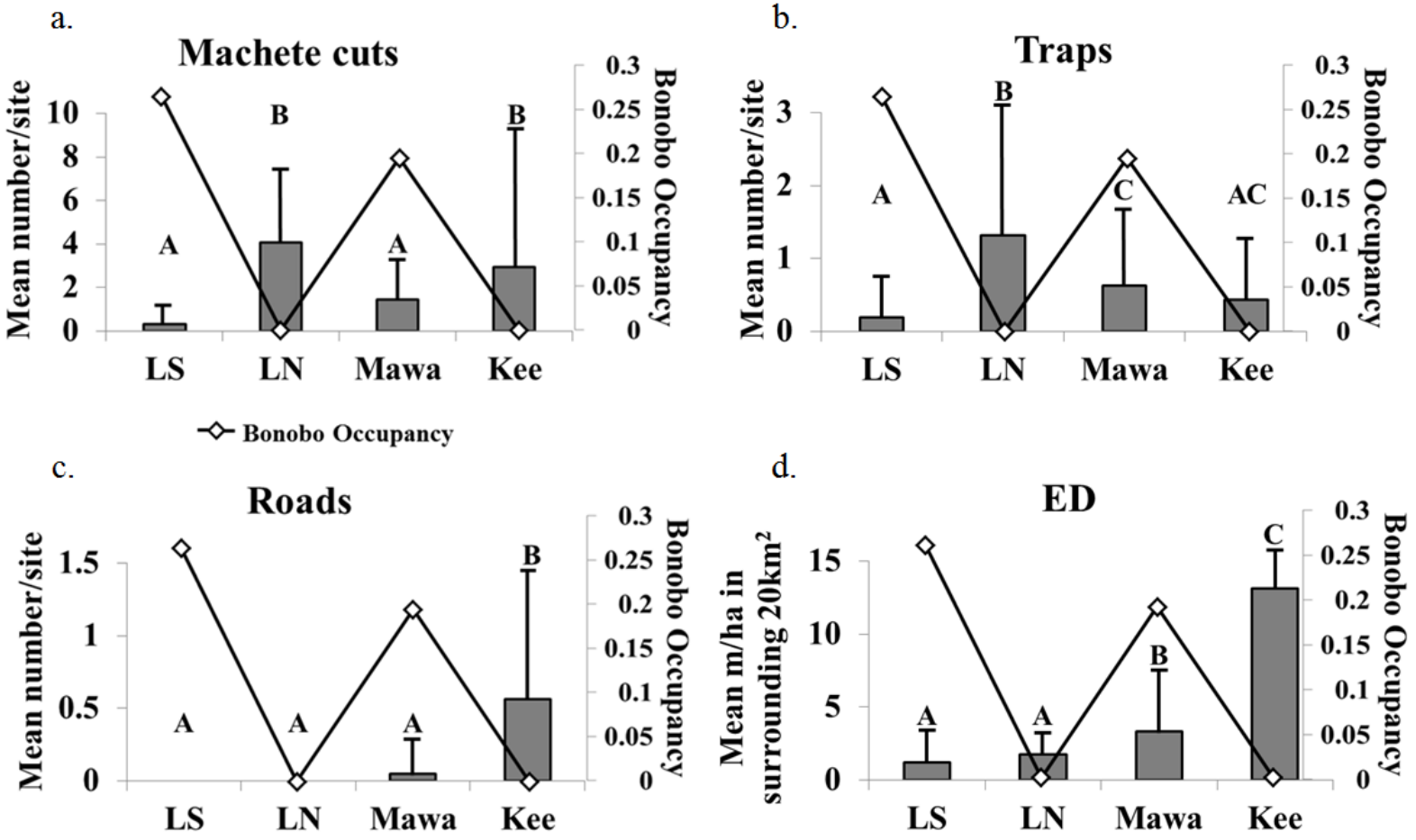

Figure 4.2. Bonobo site occupancy, mean number of human signs, and mean edge density (ED) by region in the Maringa-Lopori-Wamba landscape, Democratic Republic of Congo. Region names abbreviated as follows: LS=Lomako South and LN=Lomako North.

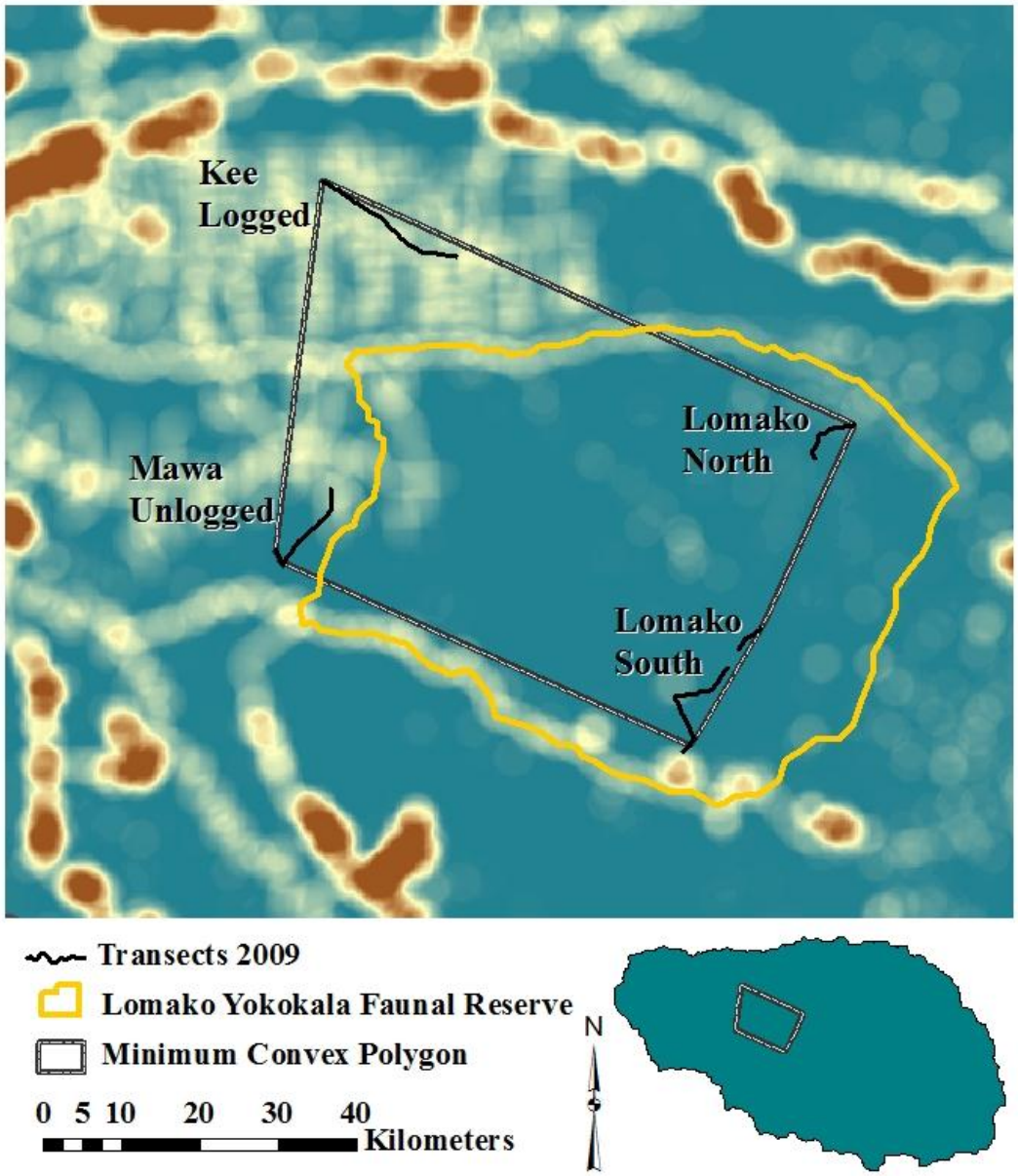

Figure 4.3. Minimum convex polygon containing the 2009 survey transects in four regions of the Maringa-Lopori-Wamba landscape, Democratic Republic of Congo.

CHAPTER 5

CONCLUSIONS

The undeniable proliferation of human impact into even the most remote regions of the world forces conservation planners to "think outside the park" and to develop strategies that will help rare species persist across broad landscapes characterized by a mosaic of land uses. As with many species of conservation concern, governmental and non-governmental organizations (NGOs) at local, national, and international levels are grappling to determine priority areas for research, monitoring, and protected-area designation for bonobos (Luetzelschwab 2007). In addition, community-based natural resource managers seek information to guide reasonable placement of protected areas and limitations of land uses potentially impactful to bonobos such as farming, logging, and housing that together are known as the sylvo-agro-pastoral zone (Dupain *et al.* 2009; USAID 2012).

A meeting to plan bonobo conservation action was held in Kinshasa, DRC in January 2011, with a large group of bonobo experts, including representatives from DRC's Institution for the Conservation of Nature (Institut Congolais pour la Conservation de la Nature, ICCN). One of several objectives identified to promote bonobo conservation was the development of strategic land-use management plans at local, regional and national levels. Achieving this objective requires spatial information about the probability of bonobo occurrence, not only in surveyed areas, but in the vast unsampled areas as well. Broad-scale, species-specific landscape metrics and models can provide needed information when they are grounded in field-based data regarding species occurrence and local environmental conditions.

For species affected by hunting, the empty forest syndrome (Redford 1992, Fa and Brown 2009, Wilkie *et al.* 2011) complicates predictions of species occurrence based solely on the presence of ostensibly suitable habitat. Viewed from satellites, intact forests can mask defaunation caused by hunting. Therefore there is a need to assure that predictions of bonobo occurrence based on remotely-sensed data are verified in the field. The recent collaboration of bonobo researchers, who compiled 10 years of bonobo data rangewide (Chapter 3), provided an opportunity to test the utility of remotely-sensed data in predicting bonobo occurrence against known bonobo locations and local evidence of hunting threats (Chapter 4).

While satellite imagery cannot detect hunting explicitly, remote sensing can capture the forest fragmentation that exacerbates hunting and pet trade activities. Across taxa, the preponderance of fragmentation studies focus on highly disturbed landscapes in which habitat occurs in isolated patches surrounded by a matrix of non-habitat (Andrén 1994, Fischer and Lindenmayer 2007, Arroyo-Rodriguez *et al.* 2008) as well as on species that are habitat specialists adverse to openings in their habitat. Our study takes a different approach, investigating the potential consequences of habitat fragmentation prior to the matrix transitioning from habitat to non-habitat (sometimes called perforation) and focusing on a vagile species tolerant of forest openings (when not hunted). We hypothesized that increased bonobo avoidance of perforated forests due to increased hunter access and/or increased hunting mortality near openings to be a likely mechanism by which forest fragmentation could influence the distribution of the highly mobile bonobo.

At the landscape and rangewide scales, we evaluated the accuracy of numerous metrics derived from remote sensing to predict bonobo occurrence. Of the factors examined, the most important predictors influencing the bonobo distribution at the rangewide scale were distance

from agriculture, fragmentation, and percent forest. Distance from agriculture was by far the strongest predictor of bonobo presence, with probability of suitable conditions increasing farther from agriculture. However, at regional scales within different landscapes, we showed these best predictors can rank differently in importance. For instance, fragmentation was the most influential metric for predicting bonobo occurrence in the Maringa-Lopori-Wamba (MLW) landscape in the north-central portion of the range, yet had relatively low predictive importance for the Tshuapa-Lomami-Lualaba (TL2) landscape in the southeastern portion of the range.

At yet finer scales, comparisons between regions within MLW underscored the importance of both field-derived and remotely-sensed predictors. Our results corroborated other research (Hart *et al.* 2008) that hunting can reduce bonobo occurrence in the absence of fragmentation yet also demonstrated that higher fragmentation correlates with lower bonobo occurrence when comparing areas with similar hunting pressure.

Future research should strive to clarify the causal links connecting landscape metrics and bonobo distributions. Are fragmented forests less occupied primarily due to increased hunting pressure or are there other ecological characteristics of fragmented forests that help explain reduced bonobo occurrence? Furthermore, due to the large extent of the bonobo range and the apparent variability of fragmentation levels tolerated by bonobos inhabiting different regions, it is worth exploring the relationships between specific bonobo sub-populations and landscape variables such as fragmentation. Differences in species or phenology of fruiting trees, forest structure, hunting pressure, or behaviour of bonobos could contribute to the differences we documented in the predictive power of fragmentation between regions.

Finally, it is important to acknowledge that while some models are useful, all models are simplifications of the real world with inherent error. Therefore, we urge field surveys of areas

with both low- and high-suitability based on the models presented here, perhaps with a larger proportion of the effort in the higher probability locales. Such surveys would provide needed data to either verify or refine the models for improved prediction and understanding. Such field surveys may identify previously undocumented bonobo groups, and where intact forest is found devoid of bonobos, field surveys can contribute further data regarding the hunting pressure and environmental conditions that may explain empty forests. Because forests and bonobo populations are dynamic systems, we advocate long-term repeated studies in order to build datasets that can elucidate causal mechanisms of empty forests as well as factors contributing to high bonobo occupancy.

Documenting high hunting pressure in otherwise intact, remote forest can bolster the case for increased enforcement and proactive conservation in specific areas. In that regard, we documented very high hunting pressure within the northeast portion of the Lomako-Yokokala Faunal Reserve correlated with very low bonobo occurrence. We recommend that the ICCN and NGOs in MLW increase funding, training, and enforcement patrols in this portion of the landscape. Regular boat inspections and contraband confiscations on the Yokokala River should discourage illegal bushmeat traffickers sourcing their meat from the Reserve.

We recommend a two-pronged approach to conservation action, as enforcement will not suffice. Where possible, future sylvo-agro-pastoral zones should concentrate in areas of least suitability while avoiding areas of high suitability as predicted by the rangewide bonobo occurrence model presented here. Conservation planners can encourage proactive management of land uses such as logging and agriculture and strategic placement of protected areas and hunting areas in an effort to meet local communities' needs while doing the least harm to bonobo populations.

Our approach for evaluating the utility of landscape-level metrics and models to predict species occurrence can be applied to taxa of conservation concern globally. Landscape metrics can be developed for a given species by classifying habitat specifically with that species' needs in mind and by selecting a window size at the scale that the species likely responds to the metric being tested (perhaps the scale of the species' homerange). These metrics can be ranked using field data to evaluate their utility in predicting species occurrence and made spatially explicit in maps. For land managers and conservation planners, we have outlined some defensible ways to identify threshold values of landscape metrics for a given species. When delineating such thresholds we suggest employing species occurrence records that likely indicate areas of quality habitat rather than areas used in a transient manner. For example, we used nests where bonobos seek shelter for the night. The appropriate type of sign will depend on individual species' habits and needs. In addition, species-covariate relationships may change over time, especially as land use and climates shift, therefore repeated studies examining such relationships are warranted.

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