Modelling the range-wide distribution of bonobos

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Cercle Elaïs

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MODELLING THE RANGE-WIDE DISTRIBUTION OF BONOBOS

Introduction

On January 14–18, 2011, the Department of Primatology of the Max Planck Institute for Evolutionary Anthropology facilitated a workshop in Kinshasa, DRC, to collect and synthesize bonobo survey data across all field sites in the DRC and to work toward the completion of a preliminary model to predict the probability of bonobo occurrence across its historic range. In total, 16 people attended representing 10 institutions and organizations (Table 1).

Table 1: Participant list

Participant	Organization
Ashley Vosper	Wildlife Conservation Society (WCS)
Gay Reinartz	Zoological Society Milwaukee (ZSM)
Guy Tshimanga	World Wide Fund for Nature (WWF)
Hjalmar Kühl	Max Planck Institute for Evolutionary Anthropology (MPI)
Inogwabini Bila-Isia	World Wide Fund for Nature (WWF)
Janet Nackoney	University of Maryland (UMD)
Jena Hickey	University of Georgia (UGA)
Joel Masselink	Wildlife Conservation Society (WCS)
John Hart	TL2 Project, Lukuru Foundation
Nicolas Mwanza Ndunda	Bonobo Conservation Initiative (BCI)
Mbangi Mulavwa	Centre de Recherche en Ecologie et Foresterie (CREF)
Omari Ilambu	World Wide Fund for Nature (WWF)
Patrick Guislain	Zoological Society Milwaukee (ZSM)
Robert Rose	Wildlife Conservation Society (WCS)
Valentin Mbenzo	World Wide Fund for Nature (WWF)
Valentin Omasombo	Institut Congolais pour la Conservation de la Nature (ICCN)

During the first two days of the workshop, participants spent substantial time compiling, standardizing and synthesizing bonobo field data, importing it into a Geographic Information System (GIS), and assessing data gaps. In addition, the workshop participants examined and selected a suite of spatially-explicit environmental covariate datasets important for mapping and modelling bonobo habitat such as land cover type, locations of rivers, the geographic boundaries of the bonobo range, and locations of human-based features such as roads and settlements (see *Bonobo Data Compilation*).

During the second half of the workshop, participants divided into several groups according to identified tasks and targeted expertise. One group continued to work on data compilation and production of maps highlighting the geographic distribution of bonobo field data collected across the bonobo range. A second group worked on the preparation of a spatially-explicit model predicting bonobo abundance and density. Finally, a third group developed a spatially-explicit model predicting the probability of bonobo occurrence, or habitat suitability, across the bonobo range (Table 2). Preliminary results of this model are explained in the *Modelling* section.

Table 2: Schedule and Program of Workshop

Day	Objective	Tasks	Who	Outcome
14–15 January	Compilation of bonobo survey data	Compilation and standardization of datasets	Entire group	Excel list of all known bonobo survey datasets (Appendix 1); Polygon layer of all bonobo survey areas (Table 3; A.P.E.S. http://apesportal.eva.mpg.de/); Archive of all bonobo survey data
16–18 January	1. Creating range-wide maps of bonobo data	1. Overlay of suitable bonobo survey data and contextual layers	Split into groups	Set of range wide maps showing bonobo survey data availability (Figs. 1–5; A.P.E.S. http://apesportal.eva.mpg.de/)
	2. Evaluating potential for bonobo density model	2. Identifying suitable datasets and their spatial extent		Several GIS layer for inclusion in A.P.E.S. (Table 3; A.P.E.S. http://apesportal.eva.mpg.de/)
	3. Developing a bonobo occurrence model	3. Compilation of presence data; Analyses in MAXENT		Range wide bonobo occurrence layer (Table 3; Figure 6; A.P.E.S. http://apesportal.eva.mpg.de/)

Bonobo Data Compilation

Prior to the workshop, individual owners of all field survey data collected were contacted and asked for the contribution of their data. Surveys were sent out to participants asking for summary information about their bonobo field data and a standardized worksheet was included for the reporting of each participant's data. Not all field sites responded, however, so a significant amount of this work was done during the workshop. During this process, 68 historic and recent bonobo field survey datasets were identified and compiled (see Figure 1). All datasets were listed in an Excel sheet with summary information, including location and name of each data survey site, date of data collection, point of contact, etc. All compiled bonobo survey data are currently archived in the Ape Populations, Environments, and Surveys (A.P.E.S.) database (see A.P.E.S. database and A.P.E.S. portal). Based on the compiled datasets, several GIS layers were generated during both the preparatory process and the workshop (see Table 3).

A.P.E.S. database and A.P.E.S. portal

All compiled bonobo survey datasets have been archived in A.P.E.S. (http://apes.eva.mpg.de) and the derived GIS layers (Table 3) and contextual datasets are available in the A.P.E.S. portal (http://apesportal.eva.mpg.de/).

Table 3: GIS layers generated from the compiled bonobo survey data

Name of layer	**Description**	**Figure**
Surveyed areas, 2004–2010	Polygon shapefile with Minimum Convex Polygons for each surveyed area	Figure 1
Survey data availability	Polygon shapefile based on 'Surveyed areas, 2004–2010', but presenting survey areas as 10x10km grid	Figure 2
Locations of confirmed bonobo presence, 2004–2010	Point shapefile showing all locations of confirmed bonobo presence, 2004–2010	Figure 3
Locations of confirmed bonobo presence, 1980–2004	Point shapefile showing all locations of confirmed bonobo presence, 1980–2004	Figure 3
Locations of confirmed bonobo presence before 1980	Point shapefile showing all locations of confirmed bonobo presence before 1980	Figure 3
Survey priorities	Polygon shapefile containing four classes of 10x10km grid cells showing areas with confirmed bonobo presence/absence and predicted high, medium and low bonobo occurrence suitability in unsurveyed areas (modelled using MaxEnt)	Figure 4
Bonobo occurrence Probability	Raster layer at 500m resolution showing predicted bonobo occurrence probability based on set of environmental predictors (modelled using MaxEnt) (Table 4)	Figure 5

Figure 1: Map showing minimum convex polygons for bonobo survey areas (2004–2010)

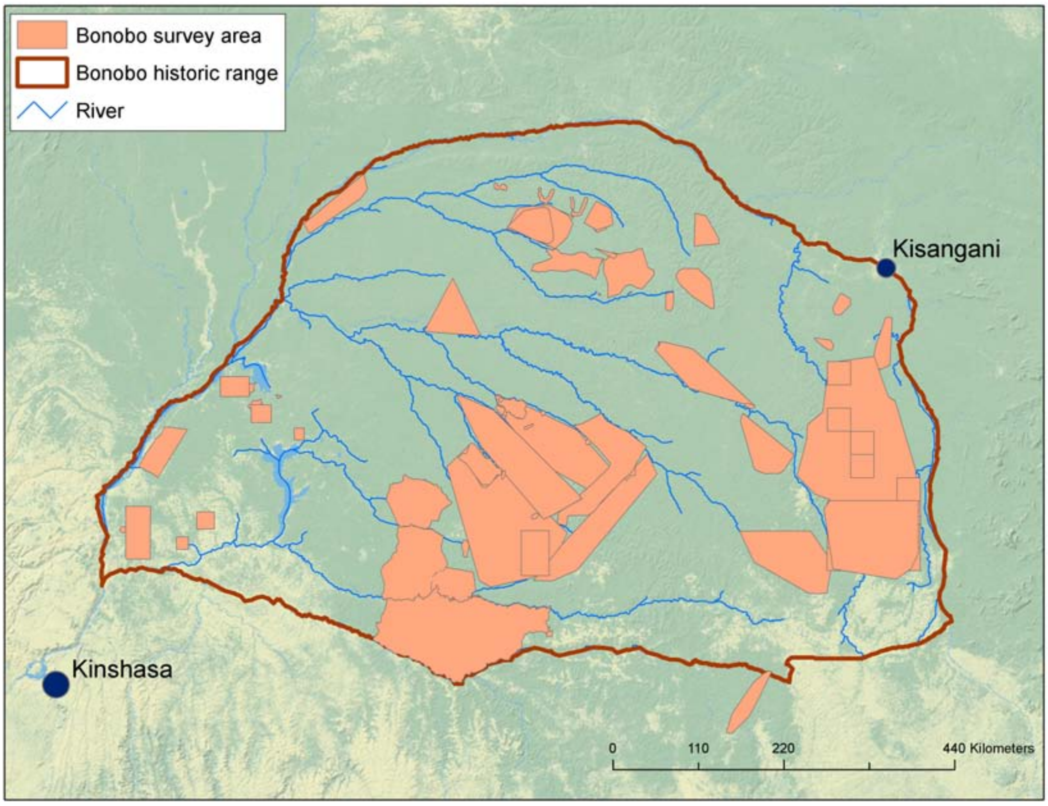


Figure 2: Map showing bonobo survey data availability 2004–2010 as grid

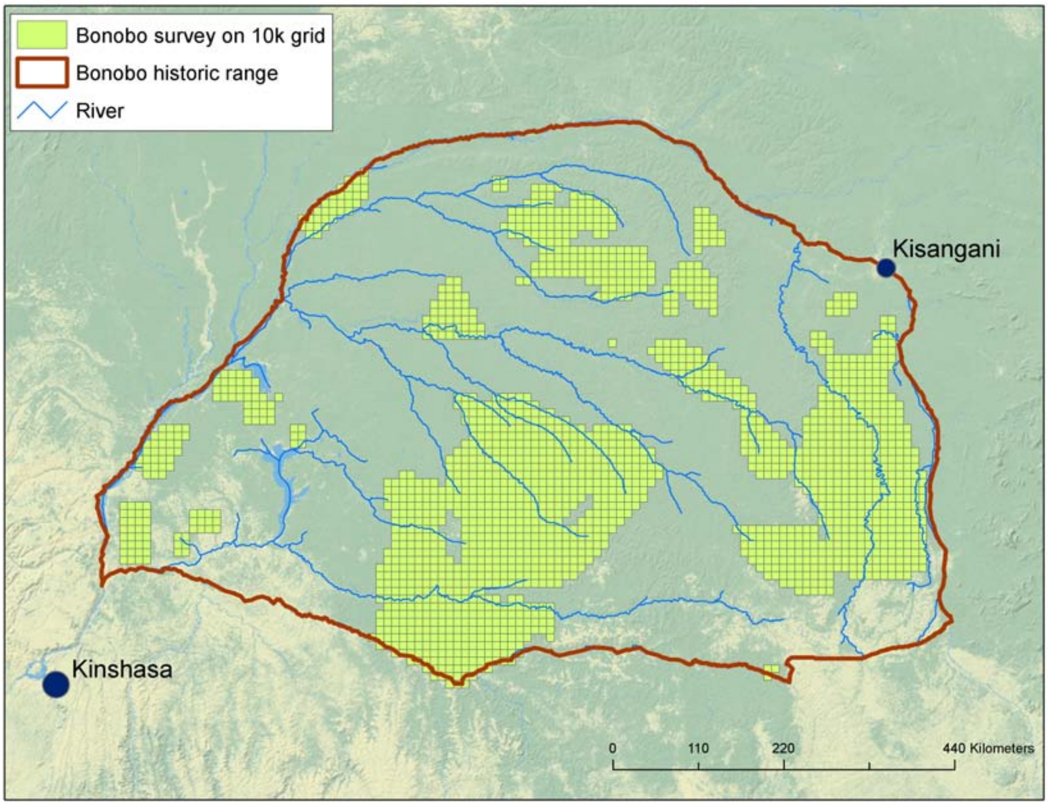


Figure 3: Map showing confirmed bonobo presence locations for three time periods

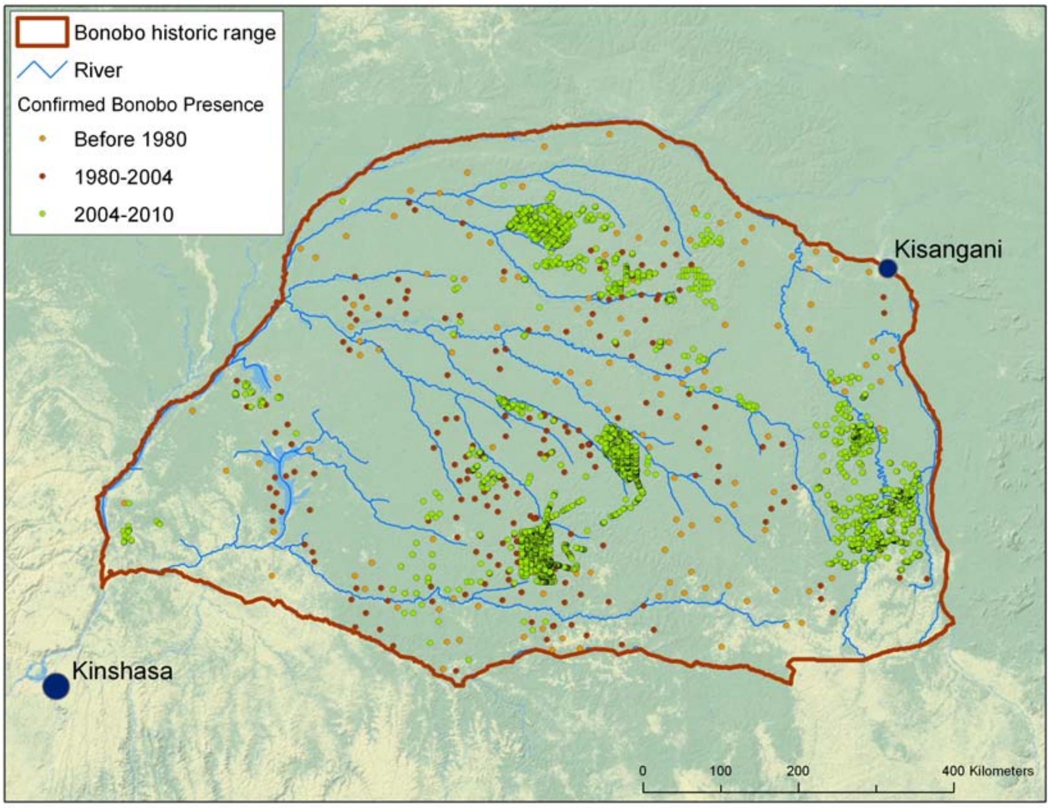
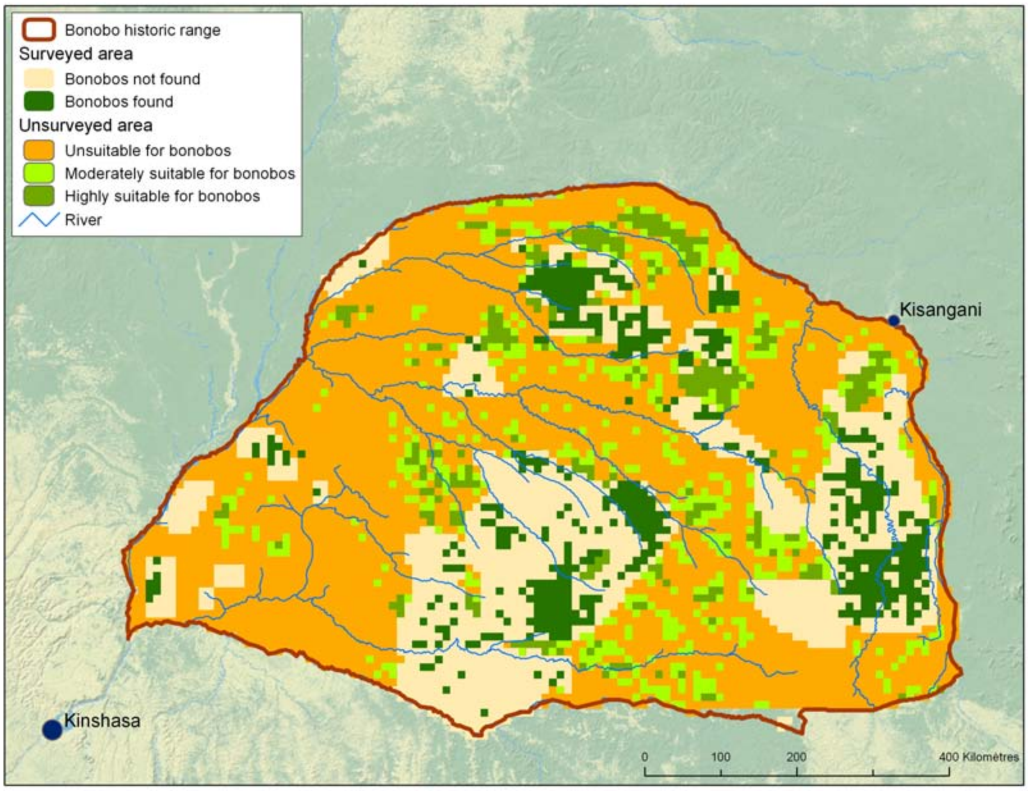


Figure 4: Map showing bonobos observed and not observed in surveyed areas and probability of suitable conditions, from Maxent model for unsurveyed areas. Please note that few datasets were not included in this map due to time constraints at the end of the workshop. An updated version is in progress.



Bonobo density and abundance estimates

After initial screening of available datasets to evaluate the potential to develop a range-wide bonobo density estimate, we concluded that there are currently too few appropriate datasets to create a robust model based range-wide predictions of bonobo density. However, this might change in the future with new field surveys currently taking place.

Modelling Bonobo Distribution

Introduction and Goals

During the second half of the workshop, a select group of participants worked to develop a spatially-explicit model predicting the probability of bonobo occurrence across its range. The model was developed using a modelling software tool called MaxEnt (Phillips *et al.,* 2006). Model inputs, methods, and preliminary results are described here. The overall objectives of the modelling process included: to understand and describe the geographic distribution of bonobos; to identify the factors that influence the current bonobo distribution; and to provide a tool which could aid in identification of high priority areas for bonobos and future bonobo conservation.

Predictor Variables

A suite of spatially-explicit environmental predictor data was identified and compiled according to the anticipated relevance to bonobo habitat suitability. A list of the data selected, along with their corresponding sources, is shown in Table 4. Data were divided into five categories: forest metrics, topography, hydrography, climate, and human impact. Each dataset was resampled to 500-meter resolution and used as input in the MaxEnt model.

Bonobo presence locations

All available bonobo presence data were compiled into a single spreadsheet with standardized identification information including the name of the site where the data were collected, the latitude and longitude coordinates of the presence points, the date and time of data collection, the type of bonobo presence detected (i.e., nest site, feeding sign, vocalization, tracks, etc.) and its age (fresh, recent, old, very old). In all, 68 different bonobo datasets were collected and compiled, representing 63 different field sites.

Table 4: List of Environmental Predictor Variables

Category	Variable Name & Description	Source
Forest metrics	Landcover classification	Food and Agriculture Organization (FAO) of the United Nations. 2000. Africover Multipurpose Land Cover Databases for Democratic Republic of Congo. Rome: FAO. Online at www.africover.org
Forest metrics	Presence of intact forest blocks (> 500 km2)	Potapov P., Yaroshenko A., Turubanova S., Dubinin M., Laestadius L., Thies C., Aksenov D., Egorov A., Yesipova Y., Glushkov I., Karpachevskiy M., Kostikova A., Manisha A., Tsybikova E., Zhuravleva I. 2008. Mapping the World's Intact Forest Landscapes by Remote Sensing. Ecology and Society, 13 (2)
Forest metrics	Forest edge density (forest fragmentation), derived by Hickey *et al.* (in prep.) using FRAGSTATS	Based on Hansen, M.C., Roy, D., Lindquist, E., Justice, C.O., and Altstatt, A. (2008). A method for integrating MODIS and Landsat data for systematic monitoring of forest cover and change in Central Africa. Remote Sensing of Environment, 112 2495-2513.
Topography	Elevation determined from a 1-km Digital Elevation Model	U.S. Geological Survey Centre for Earth Resources Observation and Science (EROS), HYDRO1k Elevation Derivative Database. Sioux Falls, SD
Topography	Soil lithology	The Soil and Terrain database for Central Africa (SOTERCAF, version 1.0), FAO and ISRIC World Soil Information 2006/2007
Topography	Dominant soil types	The Soil and Terrain database for Central Africa (SOTERCAF, version 1.0), FAO and ISRIC World Soil Information 2006/2008
Topography	Compound Topographic Index	U.S. Geological Survey Centre for Earth Resources Observation and Science (EROS), HYDRO1k Elevation Derivative Database. Sioux Falls, SD
Hydrography	Distance to rivers and streams at 500m resolution	U.S. Geological Survey Centre for Earth Resources Observation and Science (EROS), HYDRO1k Elevation Derivative Database. Sioux Falls, SD
Human Impact	Distance from rural areas (agriculture), mapped at 500m resolution	GlobCover Land Cover v2.3 2009 database. European Space Agency and UCLouvain. 2010. Downloadable at: http://ionia1.esrin.esa.int/index.asp

Human Impact	Distance from roads, mapped at 500m resolution	World Resources Institute and the Ministry of the Environment, Conservation of Nature and Tourism of the Democratic Republic of Congo. 2010. Atlas forestier interactif de la République Démocratique du Congo - version 1.0. Washington, D.C.: World Resources Institute. Downloadable at: http://www.wri.org/publication/interactive-forest-atlas-democratic-republic-of-congo
Human Impact	Presence of and distance to forest loss 1990–2000 and 2000–2010	Potapov, P., Turubanova, S., Adusei, B., Bongwele, E., Amani, P., Hansen, M. South Dakota State University, the Observatoire Satellital des Forêts d'Afrique Centrale (OSFAC) and the University of Maryland

Methods

We used a machine-learning approach called maximum entropy (MaxEnt; Phillips *et al.* 2006) to develop a species distribution map for bonobos based on relationships between known nest locations and the above environmental variables. MaxEnt (version 3.3.1) is a spatially-explicit modelling 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 variable across the area of interest. MaxEnt then compares the environmental values at nest locations to the full range of environmental values observed throughout the area of interest to predict probability of nest occurrence across the bonobo range. We used bonobo nest locations rather than all signs of presence (e.g. feeding remains, tracks, vocalizations, etc.) in an effort to characterize areas of quality bonobo habitat rather than areas that bonobos may move through in a rapid or transient manner.

We ran a series of MaxEnt models at 500-m resolution varying the suite of included environmental variables, evaluated the outputs, and determined the most plausible model for current range-wide bonobo distribution based on model diagnostics (explained below). For each MaxEnt analysis in the series, we used a random 70% of the input nest-location data (or "training" data) to build the model and withheld 30% to independently test the accuracy of the model. We ran sequential analyses, first varying the input layers and then varying the input nest locations. Varying the input environmental layers allowed us to compare model performance using different predictor variables. Withholding nest-locations from specific areas allowed us to evaluate how well a given model predicted probable habitat in the area where nest locations were withheld and to conduct an informal sensitivity analysis to understand how certain highly-sampled sites might bias the model results. We tested a succession of separate models while withholding nest data from each of the following areas one at a time, respectively, Salonga, TL2 and RFLY (Lomako-Yokokala Faunal Reserve), all highly-sampled sites.

In addition, we ran the jackknife procedure in MaxEnt to help determine the relative contribution of each predictor variable. In this procedure, one variable is removed from the collection of variables and the model is run on both the individual variable and the remaining variables. With this approach, MaxEnt can calculate the difference in the gain (relative goodness of fit) of each variable alone, the model without the withheld variable, and the full model. Because MaxEnt does not generate conventional parameter estimates as in a logistic regression model, this jackknife procedure helps to describe the relative contribution of each variable to the full model.

Results

The final results of our preliminary MaxEnt model are shown in the map in Figure 5 (green areas represent highest probability of bonobo occurrence based on input data). The jackknife analysis for the results of the preliminary model showed that distance from rural areas, distance from roads, and fragmentation (as measured by edge density) were the most important predictors of bonobo nest presence (Table 5). These variables had the highest training gains when used in isolation, suggesting that, independently, they provide the most useful information of all the variables in the model. These three variables also consistently performed best, having the highest gains of all the variables tested in our series of MaxEnt models. However, although MaxEnt is fairly robust to correlation among predictor variables, such correlation can confound interpretation of variable contribution (i.e. the relative amount each variable contributes to the model). Distance from rural complexes and distance from roads were correlated. When used together in the model with other variables, distance from rural complexes appeared uniformly to contribute the most to all models, making it the most important predictor, after which the most new information came from the elevation and landcover data layers.

Certain predictor variables were removed after successive analyses because they either contributed negligibly to the models or appeared to be too highly correlated with another predictor variable. For example, forest loss between years 1990 and 2000 and between years 2000 and 2010 had training gains of less than 0.05, and likely are correlated with fragmentation (edge density), therefore they were both removed for the final model. Presence of intact forest may also be correlated with edge density and was subsequently removed, leaving edge density, the variable with the highest training gain (0.34) of the forest fragmentation metrics. Soil and lithology were expected to be correlated, so the stronger predictor, lithology was initially retained. However, lithology appeared to bias the model outputs to the sample sites, and was ultimately dropped. We expected a strong correlation between elevation and distance from river, but found that neither variable's training gain changed appreciably when the other variable was excluded from the model, therefore they were retained. Figure 6 displays the maps of all the environmental variables contained in the final model.

The most common means for evaluating the classification accuracy of the above models is with a receiver operating characteristic (ROC) plot (Figure 7). The ROC plot incorporates a black diagonal 1:1 line which equates to 0.5 area under the curve (AUC) and represents predictions no better than random. A perfect prediction would have an AUC of 1.0 with no errors of omission or commission. Our model produced AUCs of 0.855 and 0.856 for the training data and the test data respectively, indicating strong prediction accuracy. In addition, removal of one highly-sampled area at a time resulted in models that still predicted the areas of withheld data as high-probability bonobo occurrence. This demonstrated two important concepts regarding the models; (1) they predict beyond those areas where there are sample points and (2) they are fairly robust to missing data. Despite the strong performance of the final model of this workshop, we advise caution with the application of this preliminary model as further analyses and fine-tuning are planned (*see Next Step*s).

The response curves (Figure 8) show the relationship between each predictor variable and bonobo presence. As expected, distance from rural complexes was positively correlated with probability of bonobo occurrence, indicating that bonobos are nesting relatively far from concentrations of humans in rural areas. Similarly, bonobo presence was positively correlated with distance from roads. Edge density, a measure of forest fragmentation, was negatively correlated with bonobo occurrence, suggesting that bonobos tend to nest in intact forest blocks containing low edge density and not in highly fragmented forests. Land cover type and elevation appeared to serve as very broad scale predictors, simply confirming that bonobos tend to inhabit dense moist evergreen and semi-deciduous forest (represented in the bar graph titled "Vegetation cover" as value 3) and occur above approximately 400m elevation (represented in the response-curve graph titled "Elevation"). Bonobos appear to nest far from rivers more frequently than close to rivers. This may be a threat-based response similar to distance from rural areas and roads, in that higher hunting pressure can be expected near rural areas, roads and navigable rivers, all of which give humans access to areas to hunt and trap.

Model Caveats

There are several caveats to the model that are explained here. First, although our model predicts numerous unsampled areas as high-probability bonobo occurrence, there is still some potential bias due to the inclusion of highly sampled sites (i.e., Salonga, TL2 and Lomako-Yokokala). Second, nest location errors could be present due to a possible inconsistency in GPS settings used across data collection sites (for example, some sites might have used a different GPS coordinate system while collecting field data—this particular setting was not always noted in all datasets). Based on the high potential for inconsistent use of coordinate systems (projections and datums), there is a need to standardize future data collection across sites. Such standardization will make it possible for more accurate use of aggregated data across field sites. A third caveat is that some sites where bonobo nest location data have been collected were not available for use at the time of the workshop and are not yet represented in this model. Finally, because of the spatially-explicit nature of the MaxEnt tool, our use of environmental predictor variables is restricted to those data that are available across the full bonobo range as spatially-explicit data which are already in (or can be converted into) raster format. Once all bonobo nest locations and environmental data layers are fine-tuned and explored further, some areas that were initially predicted as low-probability bonobo occurrence in our model might actually change to higher probability.

Future Steps

In the coming months, more nest data will be integrated into the model and the environmental predictor variables will be continually tested for model improvement. Potential bias from highly sampled sites will also be addressed. Further investigation is needed to verify that certain predictor variables, such as distance from rural complexes and distance from roads are not too highly correlated. Additional bonobo surveys in those areas deemed highly and moderately suitable by the model (shown in green in Figure 5) would improve the strength and defensibility of the final model.

Furthermore, the workshop participants will continue their joint work by starting to publish a series of papers, all with a range-wide perspective (see Table 6). The starting point will be the publication of the range-wide Bonobo occurrence model.

Table 5: The importance of each environmental data layer in predicting bonobo occurrence.

Rank	Data	Model Gain (Importance)
1	Distance from rural areas	0.57
2	Distance from roads	0.49
3	Forest fragmentation	0.34
4	Vegetation cover (FAO-Africover)	0.27
5	Elevation	0.24
6	Distance from rivers	0.05

Table 6: Propositions for five articles on Bonobo status, threats and conservation with range-wide perspective

Subject	Description
Range-wide bonobo occurrence probability	An article on the range-wide occurrence model and the relative importance of factors influencing bonobo habitat suitability
Temporal trends in range-wide bonobo occurrence probability	An article based on the range-wide occurrence model, with the addition of a projection over time, e.g. 1990–2010
Methodological approaches for compiling and analyzing range-wide field survey data	A methods-based article using the bonobo data as an example for how to synthesize highly heterogeneous information from field surveys
Evaluating the impact of anthropogenic and environmental factors	An article on the influence of ecological variables and human impact on the density of bonobos
Developing range-wide bonobo density model	An article presenting a range-wide bonobo density model

Figure 5: Preliminary model that maps bonobo suitability across the historic range

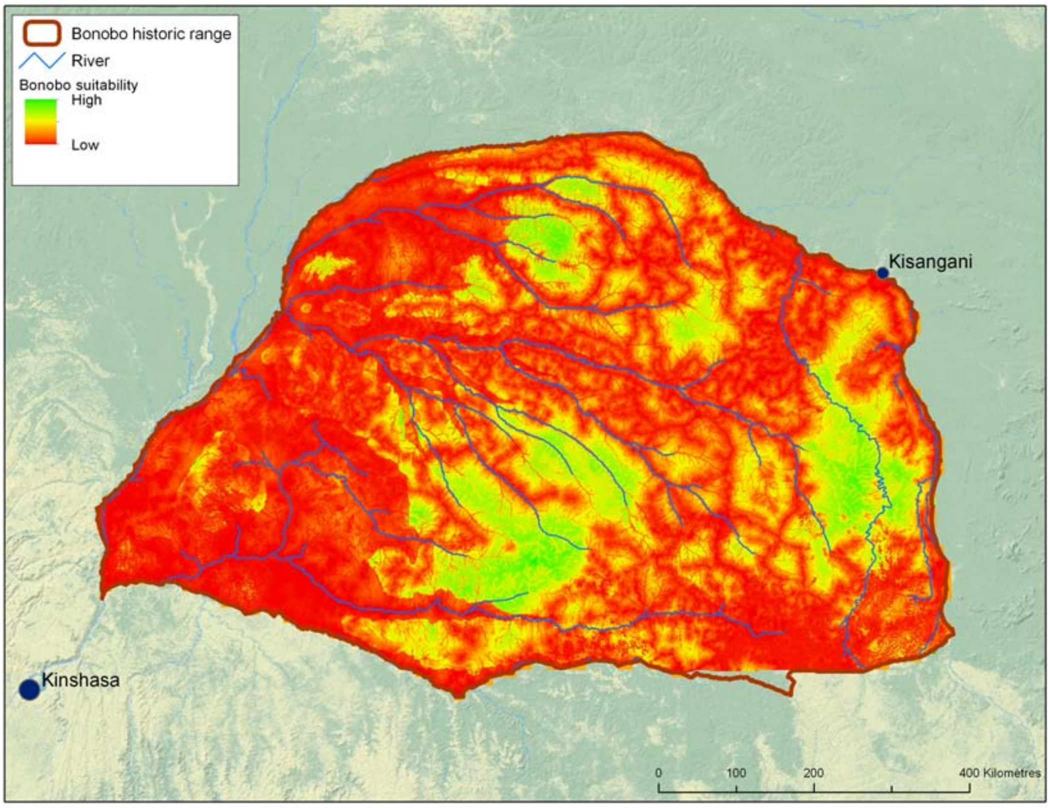


Figure 6: Environmental predictor variables used in the final preliminary model of the bonobo's range-wide distribution

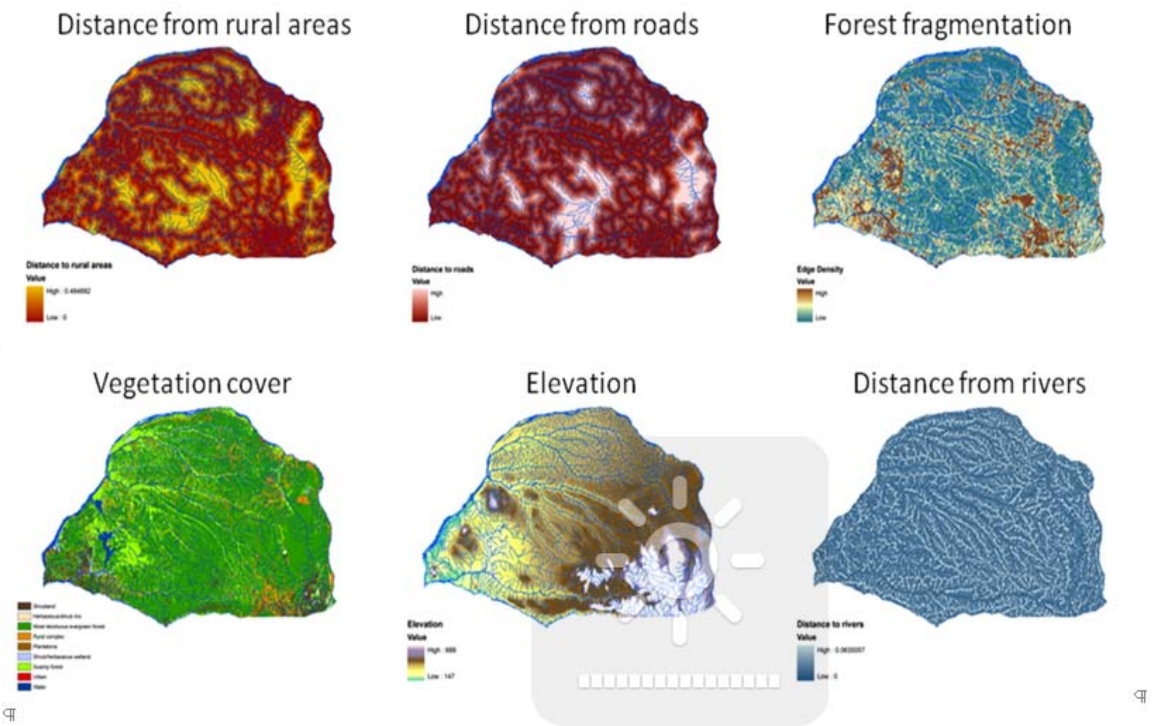


Figure 7: The Receiver Operating Characteristic (ROC) plot depicts the classification accuracy of this model. An Area Under the Curve (AUC) of 1 indicates perfect prediction. This model has a training AUC=0.855 and a test AUC=0.856, indicating a useful model.

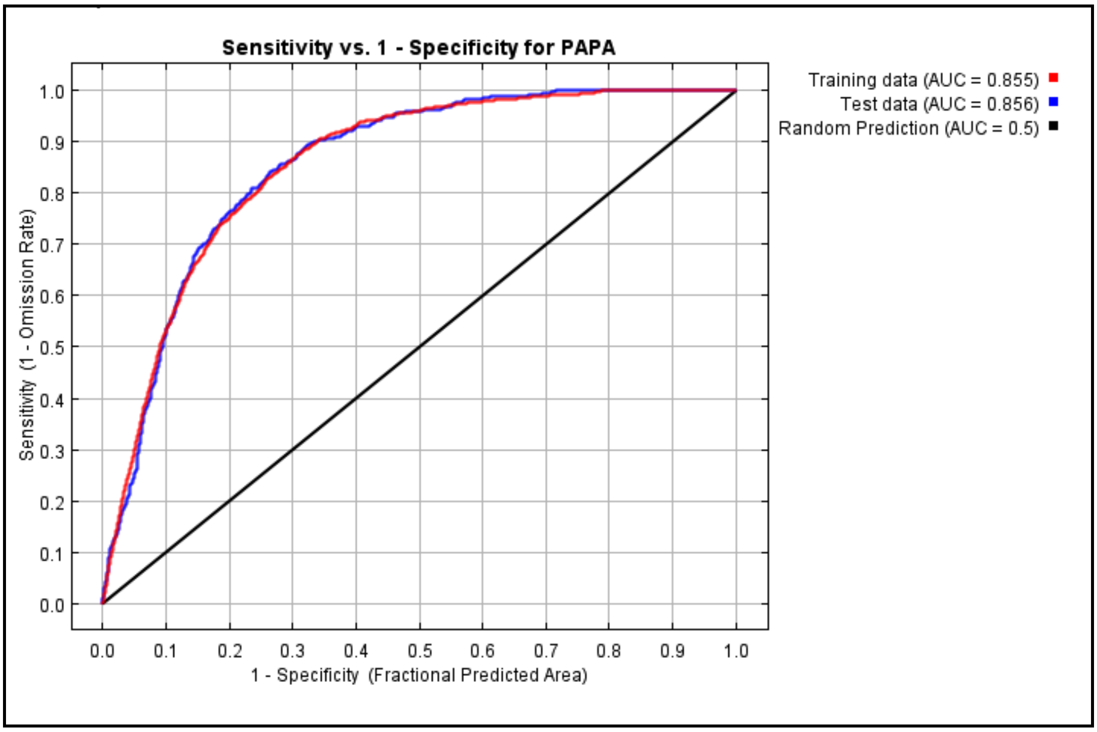
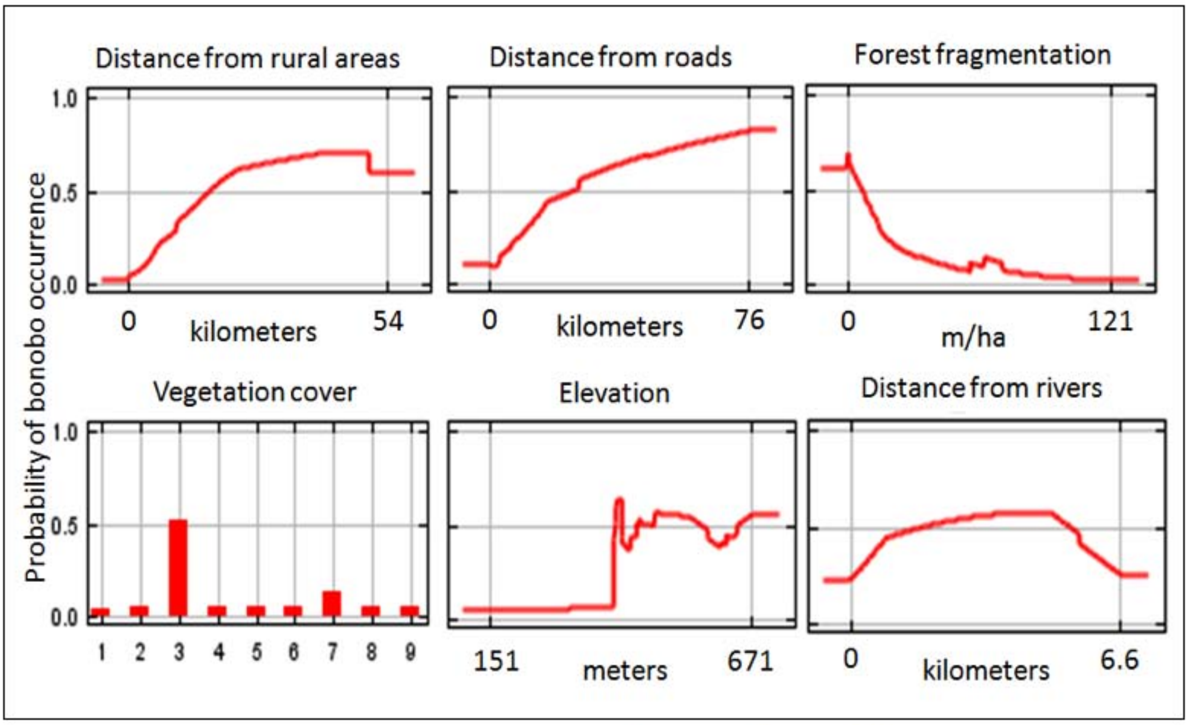


Figure 8: Response of bonobo occurrence to environmental variables in the final model. Vegetation cover category 3 represents moist evergreen and semi-deciduous forest.



Discussion

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. Now, 16 years later, a working group convened to compile and assess the completed surveys and begin to develop a range-wide understanding of bonobo distribution to inform the next bonobo action plan. Three significant goals were set for this: 1) compile the most current bonobo survey data; 2) estimate bonobo abundance and density; and 3) develop a predictive model for bonobo occurrence across the historic range.

The working group participants compiled a significant amount of survey data that had been completed since 1995. These surveys covered a substantial portion of the area recommended in Figure 10 of the 1995 Action Plan, and represent a distance of over 12,000 km (equivalent to walking from Cairo, Egypt to Johannesburg, South Africa and back). The compilation of these datasets represents the most complete and current information about bonobos across their range. Unfortunately, there were not enough data in the format necessary to develop a range-wide estimate of bonobo density and abundance, but the data were still extremely valuable in providing a better understanding of current bonobo distribution and informing the development of the predictive model.

Workshop participants used these data to develop a predictive model of bonobo occurrence probability across their historic range (as detailed above). This model accomplished two significant tasks. First, the model identifies the important factors determining current bonobo distribution, namely the distance from rural complexes, the distance from roads, the amount of forest fragmentation, and landcover. Second, the model identifies areas not yet surveyed as potentially high-quality habitat that may be important for bonobo conservation in the future. Both density estimates and the predictive model were limited by the data available, so an important next step will be to continue to build the bonobo database with existing or newly collected data in order to better inform the density estimates and the predictive model.

Beyond the accomplishments of this working group, conservationists can use these results to guide development of the bonobo conservation strategy. First, they can use the factors identified through the modelling procedure to help think about how threats across the current range impact bonobo distribution. This information, along with the threats outlined in this report, provide the necessary starting point for thinking about direct actions needed to save bonobos. Second, the results of the predictive model serve as an important indicator of where future bonobo surveys are needed. Areas of predicted high bonobo presence probability not yet surveyed may currently harbour bonobo populations. Surveys in these areas could reveal if this is the case and strengthen future models. Even without bonobos, these high probability areas could be suitable for the expansion of the current bonobo range once threats are reduced.

Geographic priorities

The picture that emerged from the modelling and our current knowledge is that there are four known areas of increased habitat suitability: the Salonga landscape, MLW, TL2 and Lac Tumba/Lac Mayombe. Using Fig. 5 above, we will be able to identify survey priorities where bonobos may occur. Following new surveys, additional priority areas may become apparent.

Priority Actions

Overall, the priority actions should focus on the need to reduce bonobo mortality caused by hunting. The usual threats to ape populations are hunting, habitat loss and disease. Currently the latter two are not major threats to bonobos, but they are likely to become more important in the future, as can already be seen by the effects of forest fragmentation on probability of bonobo presence. The modelling results strongly suggest that threats associated with human activity (distance from rural complexes, distance from roads, forest fragmentation) drive bonobo distributions, rather than biotic and abiotic factors (vegetation type, elevation, or soil). Very likely, it is the poaching associated with these different measures of human activity that is the single common threat influencing bonobo occurrence. The analysis used proxies that are widely accepted to evaluate hunting impact (e.g. distance to roads, distance to rural areas). These were the major predictors of bonobo occurrence probability, indicating that at a broad scale, poaching is the major factor determining bonobo distribution. However, at the regional/local scale, there are some exceptions to this generalisation due to cultural taboos against eating bonobos. Such taboos are in a state of flux due to the changing values associated with immigrant populations (Fruth *et al.* 2008); therefore poaching of bonobos may begin to occur in new areas, further underscoring this threat.

Acknowledgements

We would like to thank the numerous provider of Bonobo field data (appendix 1), who made their data available for this workshop and thus made it possible to take this range-wide perspective on Bonobo status. We also would like to thank Anthony Rylands and the Margot Marsh Biodiversity Foundations's Primate Action Fund for funding this workshop and Yasmin Möbius, Rebecca Kormos, Terese Hart, Liz Williamson and Valentin Omasombo for great organisational support and for preparing this workshop. We are also very grateful for the logistical support WCS provided. Last, we would like to thank Fiona Maisels, Liz Williamson and Conrad Aveling for reviewing this report and for pointing out inconsistencies in model predictions.

References

Fruth, B., Benishay, J.M., Bila-Isia, I., Coxe, S., Dupain, J., Furuichi, T., Hart, J., Hart, T., Hashimoto, C., Hohmann, G., Hurley, M., Ilambu, O., Mulavwa, M., Ndunda, M., Omasombo, V., Reinartz, G., Scherlis, J., Steel, L. & Thompson, J. 2008. *Pan paniscus*. In: IUCN 2010. IUCN Red List of Threatened Species. Version 2010.4. <www.iucnredlist.org>. Downloaded on **08 June 2011**.

Steven J. Phillips, Robert P. Anderson, Robert E. Schapire (2006). "Maximum entropy modeling of species geographic distributions." Ecological Modelling, 190:231-259.

Thompson-Handler N, Malenky RK, Reinartz GE (1995) *Action Plan for* Pan paniscus: *Report on Free Ranging Populations and Proposals for their Preservation*. Zoological Society of Milwaukee County, Milwaukee.

Appendix 1: List of all datasets provided

ID	Data provider	Organisation	Area name
1	Jena Hickey	University of Georgia	Lomako
2	John Hart/Ashley Vosper/Steve Blake	TL2 project/WCS	Salonga NP south
3	John Hart/Ashley Vosper/Steve Blake	TL2 project/WCS	Salonga NP north
4	Gay Reinartz	Zoological Society Milwaukee	Salonga_NP_Biondo_Biondo
5	Gay Reinartz	Zoological Society Milwaukee	Salonga_NP_Bonima
6	Gay Reinartz	Zoological Society Milwaukee	Salonga_NP_Ikolo
7	Gay Reinartz	Zoological Society Milwaukee	Salonga_NP_Yongo
8	Gay Reinartz	Zoological Society Milwaukee	Salonga_NP_Isanga
9	Gay Reinartz	Zoological Society Milwaukee	Salonga_NP_Beminyo
10	Gay Reinartz	Zoological Society Milwaukee	Salonga_NP_Etate
11	Gay Reinartz	Zoological Society Milwaukee	Salonga_NP_Lokofa_2002
12	Gay Reinartz	Zoological Society Milwaukee	Salonga_NP_Isaka_Bekongo
13	Gay Reinartz	Zoological Society Milwaukee	Salonga_NP_Kinki
14	Gay Reinartz	Zoological Society Milwaukee	Salonga_NP_Lotulo
15	Gay Reinartz	Zoological Society Milwaukee	Salonga__NP_Etate_Sector
16	Gay Reinartz	Zoological Society Milwaukee	MLW Corridor PA1 CBNRM
17	Gay Reinartz	Zoological Society Milwaukee	Salonga_NP_Ikolo_2005
18	Gay Reinartz	Zoological Society Milwaukee	Etate core area
19	Gay Reinartz	Zoological Society Milwaukee	Etate sector excl core area Systematic
20	Gay Reinartz	Zoological Society Milwaukee	Etate sector excl core area Habitat
21	Fiona Maisels/Innocent Liengola	WCS	Sankuru reserve
22	Fiona Maisels/Innocent Liengola	WCS	Salonga Corridor
23	Fiona Maisels/Guy Mbayma	WCS	Salonga East

24	Fiona Maisels/Innocent Liengola	WCS	Salonga-Lokofa_2010
25	John Hart/Ashley Vosper	TL2 project/WCS	Salonga-Lokofa_2005
26	John Hart/Ashley Vosper	TL2 project/WCS	Salonga-Lomela 2006
27	John Hart/Ashley Vosper	TL2 project/WCS	Salonga-Iyaelima 2006
28	Ashley Vosper	WCS	Reserve de Faune de Lomako-Yokokala (RFLY)
29	Ashley Vosper	WCS	Reserve de Faune de Lomako-Yokokala (RFLY)
30	Ashley Vosper	WCS	Reserve de Faune de Lomako-Yokokala (RFLY)
31	Ashley Vosper	WCS	Reserve de Faune de Lomako-Yokokala (RFLY)
32	Ashley Vosper	WCS	Reserve de Faune de Lomako-Yokokala (RFLY)
33	John Hart/Ashley Vosper	TL2 project	Tshuapa-Lomami
34	Omari Ilambu	WWF	Lotoi-Lokoro
35	Omari Ilambu	WWF	Lokoro-Lukenie
36	Omari Ilambu	WWF	Lukenie-Sankuru
37	Nicolas Mwanza Ndunda	BCI	Nkosso
38	Nicolas Mwanza Ndunda	BCI	Botwali
39	Nicolas Mwanza Ndunda	BCI	Mbie Mokele
40	Nicolas Mwanza Ndunda	BCI	Monieke-Bokote
41	Nicolas Mwanza Ndunda	BCI	Samba
42	Nicolas Mwanza Ndunda	BCI	Lilungu
43	Nicolas Mwanza Ndunda	BCI	Lingomo
44	Nicolas Mwanza Ndunda	BCI	Sankuru reserve_Lomela
45	Nicolas Mwanza Ndunda	BCI	Sankuru reserve_Katako
46	Nicolas Mwanza Ndunda	BCI	Mompono
47	Nicolas Mwanza Ndunda	BCI	Sankuru-Lomela
48	Nicolas Mwanza Ndunda	BCI	Yetsi-Ikela
49	Nicolas Mwanza Ndunda	BCI	Lonua

50	Nicolas Mwanza Ndunda	BCI	Kokolopori bonobo reserve
51	Nicolas Mwanza Ndunda	BCI	Kokolopori summary
52	AWF	AWF	Cadjobe
53	Jo Thompson	Lukuru Project	Lukuru
54	Takeshi Furuichi	Kyoto University	Iyondji forest block
55	Takeshi Furuichi	Kyoto University	Bilya_HotSpot_Iyondje
56	AWF	AWF	MLW_1_K7
57	AWF	AWF	MLW_2_K7
58	AWF	AWF	MLW_3_K7
59	AWF	AWF	MLW_4_K7
60	Takeshi Furuichi	Kyoto University	Luo Reserve
61	AWF	AWF	Cadjobe
62	AWF	AWF	Lomako: Omasombo
63	Alain Lushimba	AWF	K7
64	AWF	AWF	K2
65	Valentin Mbenzo	WWF	Mbala-Ndongese
66	Valentin Mbenzo	WWF	Botuali-Ilombe
67	Valentin Mbenzo	WWF	Ngombe-Botuali
68	Valentin Mbenzo	WWF	Malebo-Nguomi (Nkala, Nkoo, Mpelu, Embirima,...)
69	Valentin Mbenzo	WWF	Bopaka
70	Valentin Mbenzo	WWF	Kenia
71	Valentin Mbenzo	WWF	Mampoko (Bolombo-Losombo)
72	Valentin Mbenzo	WWF	Mpoka (Mompulenge-Mbanzi)
73	Omari Ilambu	WWF/Sodefor	Luna
74	RKK	SCP	Kutu_Luna
75	RKK	SCP	Kutu_Lola
76	RKK	SCP	Kutu_Illomo
77	RKK	SCP	Kutu_Isaka

78	RKK	SCP	Kutu_Lumokita
79	RKK	SCP	Kutu_Lokumou
80	RKK	SCP	Kutu_Bekolo
81	NA	NA	Mushi
82	John Hart	TL2 Project	Lusambo
83	Jonas Eriksson	NA	several_sites_Jonas
84	Gottfried Hohmann	MPI	LuiKotale
85	Omari Ilambu/WWF	WWF	Bolobo
86	Caldecott	NA	Salonga
87	Kortlandt	NA	rangewide
88	Schouteden	NA	rangewide