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## Research Article

# Movement and occurrence of two elephant herds in a human-dominated landscape, the Bénoué Wildlife Conservation Area, Cameroon

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### Abstract

Increasing human settlement and disturbance adjacent to protected areas have intensified competition between people and wildlife for resources and living space. In northern Cameroon, over 60,000 people live in villages surrounding Bénoué National Park. In that same area, as in other parts of Africa, savanna elephants damage crops, homes, water provision infrastructures, and grain stores. Using almost 1000 satellite-derived positions for two matriarch female elephants from 2007 to 2009, movement patterns were analyzed with respect to a highway, secondary roads, unpaved park roads, rivers, and villages through the use of log linear modeling. More than half of all locations and core areas occurred outside the park, while seasonal and individual differences in home range size and distribution were found within the protected area. Elephant occurrence within approximately 7 to 9 km of villages showed a decreasing trend with proximity. The highway appeared to act as a barrier to movement for one elephant herd, while the other did not come within 11 km of it. On the other hand, elephants remained close to the Bénoué River and secondary roads. Our findings show that in the Bénoué Wildlife Conservation Area, perennial water availability and human disturbance from the presence of villages can influence elephant spatial distribution in the protected area, and overlap of villages with elephant home range indicates a high potential for human-elephant conflict. This highlights the need for more effective land use planning to reduce such conflict and for additional research into movement patterns of the Bénoué National Park elephant population.

**Key words:** Cameroon, elephant, GIS, home range, movement

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## Introduction

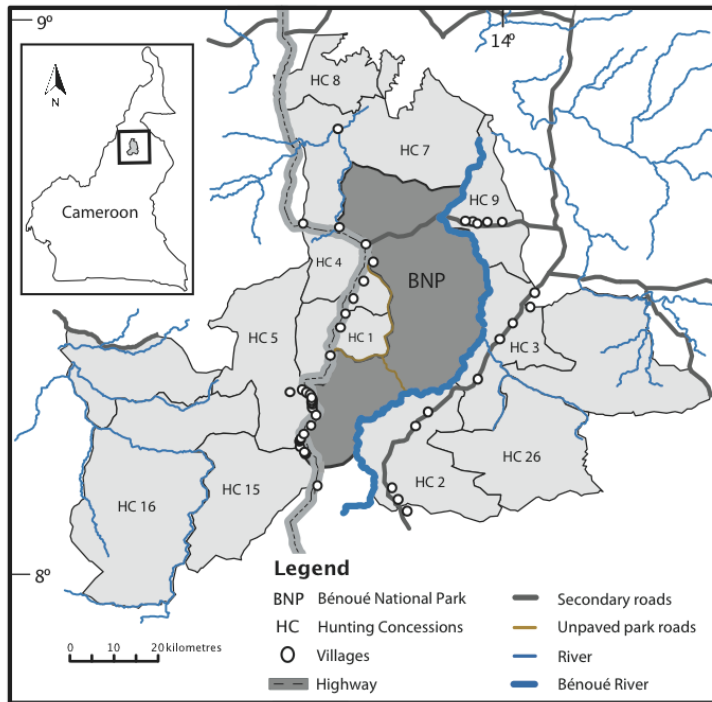
With 80% of African savanna elephant (*Loxodonta africana*) range found outside protected areas [1], overlap with human settlement is inevitable, leading to conflict between species through competition for land and resources [2, 3]. Consequences include elephants causing human injury or death and destroying water and/or grain supplies [4]. Elephants also damage crops when they leave the refuge of parks and/or wildlife reserves and travel through human communities; growing settlement and land conversion adjacent to these areas exacerbates the problem [1, 5-7]. This can lead to illegal hunting by villagers to eliminate elephants thought to be recurring crop raiders [8,9]. Hunting is of special concern where elephant numbers are declining, such as in Central Africa [10], as populations can be sensitive to even minimal increases in cow mortality [4]. Human activity, particularly in unprotected areas, may therefore determine elephant distribution and threaten the long-term viability of elephant populations [11].

The ability to identify areas that may be at high risk of human-elephant conflict (HEC) is important in preventing further elephant population decline in Central Africa. Threatened by poaching, habitat loss, and ongoing conflict with people [12], the elephant population in Central Africa is estimated to number 1500 and is thought to have decreased by at least 76% within the last forty years, with more pronounced declines over the last decade [13]. Determining elephant spatial use of areas in and around protected areas and understanding the influence of human presence must therefore be considered in efforts to mitigate damage and reduce conflict [14]. In this study, we use almost 1000 locations between two female elephants of distinct herds to describe their movement patterns in and around Bénoué National Park (BNP), Cameroon. In particular, we use Argos satellite technology to determine home range size and spatial use of the protected area, along with elephant occurrence relative to roads, villages, and rivers (primarily the Bénoué River). Additionally, we evaluate the potential for HEC in this area in relation to previous local reports of crop raiding by wildlife [15].

## Methods

The Bénoué Wildlife Conservation Area (BWCA) consists of Bénoué National Park (7.55°-8.40°N; 13.33°- 14.02°E) and eleven surrounding hunting concessions (HC) (Fig. 1). BNP covers 1800 km<sup>2</sup> of the conservation area's 8438 km<sup>2</sup>. Nine of the HC border the park, acting as transitional land between the protected area and crop fields. Regulated hunting is allowed in the HC, and although not legally permitted, settlement, agricultural and forestry activities occur there as well. Over 60,000 people (mostly agriculturalists) live in villages largely surrounded by crop fields throughout the HC [16]. This area is classified as part of the East Sudanian Savanna Ecoregion. The wet season occurs from May to September, while the dry season lasts from October to April.

The BNP elephant population was recently estimated at approximately 540 [10]. Two adult female elephants (named Doudjatou and Oldiri) from different herds in BNP were collared in April 2007 near the villages of Doudja and Mbaou, respectively, and their locations were tracked using Argos satellite technology. Females were chosen because of the matriarchal nature of elephant societies, where elephants live and travel in herds led by an older cow. Following observations, Doudjatou and Oldiri were selected as the individuals to be fitted with radio collars because, as the largest females in their respective herds, they were presumed to be the matriarchs. Herds generally include several related females, their daughters, and juvenile sons, with groups averaging around nine individuals [17]; locations of a single female are therefore representative of the entire herd [18-20]. At the time of capture, Doudjatou was observed with a herd of 27 elephants, while Oldiri was seen to travel with 32 others.



**Fig. 1. Bénoué Wildlife Conservation Area in northern Cameroon, including Bénoué National Park and eleven surrounding hunting concessions, as well as villages, roads, and the Bénoué River. Inset shows the location of the study area within Cameroon.**

Once located, the two elephants were immobilized by darting with etorphine hydrochloride (Wildlife Pharmaceuticals, Fort Collins, CO, USA) and fitted with Argos satellite collars (Telonics Inc., Mesa, AZ, USA). Collaring took place in the dry season to facilitate better visibility for tracking. Collars transmitted approximately one to two locations each day starting April 17, 2007, and collar data transmission was generally around 24 hours apart, though sometimes this increased to several days. Data covered four seasons: the wet seasons of 2007 and 2008, and dry seasons of 2007 and 2008. Error was reduced by using only locations with class 2 (150 to 350 m) or 3 (<150 m) location class error margins. Data for Oldiri differed from that of Doudjatou in that location data for the dry season of 2008 were unavailable due to collar malfunction. Mean rainfall during the wet and dry seasons during the study period was 188.6 and 18.1 mm respectively (Division of Meteorology, Cameroon's Ministry of Transport).

A total of 655 and 322 locations were used in data analysis for Doudjatou and Oldiri, respectively. Identical but separate analyses were performed for each elephant. Locations were mapped and analyses were performed using ArcGIS 9.3<sup>®</sup> (ESRI, Inc., Redlands, CA). All statistical tests were done using SAS v. 9.2<sup>®</sup> [21], and a significance level of 0.05 was adopted.

Overall and seasonal home ranges were calculated using the Animal Movement Analysis extension [22]. Home range estimates were calculated using the Minimum Convex Polygon (MCP) and Fixed Kernel (FK) methods, the latter of which is believed to be a more robust method of estimating home range size. Home ranges were estimated for utilization distributions of 50% and 95%, and unless otherwise noted, home range results refer to the 95% FK home range size. The 50% FK home ranges (the core areas) were used to measure the percent of elephant core areas that occurred inside the park. The FK home range bandwidth was selected using the Least Square Cross Validation method [22]. Chi-square contingency tests were used to find seasonal differences in the number of locations in the park.

Overall and seasonal elephant occurrence relative to a national highway, secondary roads, unpaved roads inside BNP, villages, and the Bénoué River was determined. The paved two-lane highway bordering the western region of the park is the principal route of travel between the towns of Garoua and Ngaoundéré and has a high volume of traffic. The unpaved roads in BNP are dirt or gravel paths, primarily used by safari hunters during the dry season or by park personnel year round. Secondary roads are mainly gravel roads and have an intermediate level of traffic relative to the highway and unpaved park roads.

Elephant avoidance of areas within 10 km of human settlements and roads has been reported elsewhere [23-25], along with a greater use of areas within 10 km of water sources [24, 26, 27]. We assessed elephant occurrence within 15 km of the highway, the nearest secondary road, unpaved park road, village, and Bénoué River. This was done for all locations and within each season to identify patterns in number of elephant locations relative to distance from a given area. Oldiri's occurrence relative to the highway was not analyzed, as she did not occur closer than 12.7 km to the highway. Data for wet and dry seasons from different years were analyzed separately, unless otherwise indicated. As the response variable -occurrence- was count-type data, analyses were done using log linear models, and occurrence was analyzed at 1 km intervals up to and including 15 km.

## Results

Individual and seasonal differences in elephant home range size and distribution were found (Table 1). Doudjatou exhibited longer distance movements to the northern park region whereas Oldiri mostly remained near the same eastern region of the park (Appendix 1). Less than half of each elephant's overall locations occurred inside BNP (Doudjatou: 45.2%; Oldiri: 35.7%; Table 1). In 2007, Doudjatou's occurrence in the park was greater in the wet season than in the dry season ( $\chi^2 = 6.29$ ,  $df = 1$ ,  $P = 0.012$ ), though no seasonal difference was found in 2008 ( $\chi^2 = 0.32$ ,  $df = 1$ ,  $P = 0.570$ ). Similarly, no seasonal difference of occurrence inside the park was found for Oldiri in 2007 ( $\chi^2 = 2.51$ ,  $df = 1$ ,  $P = 0.113$ ). Elephants also varied in how much of their core areas overlapped with BNP. Forty-one percent of Doudjatou's total core area was found in the park, while only 22.8% of Oldiri's core area was found in the park (Table 1). Core areas of both animals always included the Bénoué River, regardless of season (Appendix 1).

Doudjatou's occurrence declined with proximity to the highway, but only during the dry seasons and for locations within approximately 8 km of the highway (Appendix 2a; Table 2), with no clear trend in either wet seasons. Oldiri, on the other hand, did not come within 11 km of the highway. Elephant occurrence increased with proximity to the river (Appendix 2b; Appendix 3), and a similar trend was observed for occurrence relative to secondary roads (Appendix 2c; Appendix 3). Elephants showed different patterns in their locations relative to unpaved park roads: within 10 km, Oldiri's overall occurrence was greater near these roads, whereas for Doudjatou, the opposite trend was found (Fig. 3d; Table 2). No elephant ever crossed the highway, and secondary roads were crossed more frequently by both elephants (Doudjatou: 13.6% of all movement paths; Oldiri: 21.8% of all paths). Unpaved park roads were crossed more frequently by Doudjatou (44.3% of all paths) than by Oldiri (15.0% of all paths).

The number of each elephant's locations declined with village proximity, though this was largely for locations within 6 to 8 km of villages (Appendix 2e; Appendix 3). When all locations were considered, it was additionally found that the relationship between occurrence and distance relative to villages was quadratic for Doudjatou ( $\chi^2 = 39.04$ ,  $df = 1$ ,  $P < 0.001$ ) (Appendix 2e) and cubic for Oldiri ( $\chi^2 = 6.93$ ,  $df = 1$ ,  $P = 0.009$ ) (Appendix 2e), with most locations occurring at approximately 7 km for both.

**Table 1:** Fixed Kernel (FK) and Minimum Convex Polygon (MCP) home range sizes (Km<sup>2</sup>), along with percent of locations and percent of core areas found inside Bénoué National Park (BNP) for Doudjatou and Oldiri, within seasons and for all locations.

Season	Year	2007		2008		Both years		All locations
		Wet	Dry	Wet	Dry	Wet	Dry	
<i>Doudjatou</i>								
	95% FK	1132.08	2421.68	1093.77	2500.98	1433.47	3282.52	2808.38
	50% FK	193.90	509.66	75.10	570.10	164.22	511.67	449.91
	100% MCP	1081.47	1879.5	1020.2	2865.53	1260.00	2945.26	3171.57
	Percent of locations in BNP	60.40	44.58	40.74	40.42	42.18	44.53	45.19
	Percent of core area in BNP	60.57	33.37	45.56	38.82	28.83	37.00	41.25
	N	101	166	136	218	237	384	655
<i>Oldiri</i>								
	95% FK	1366.74	984.03	1239.61	-	1642.81	984.03	1193.58
	50% FK	194.20	141.12	134.26	-	218.26	141.12	104.26
	100% MCP	1239.82	1362.48	1074.06	-	1734.19	1362.48	2169.82
	Percent of locations in BNP	46.08	36.25	22.73	-	39.04	36.25	35.71
	Percent of core area in BNP	27.25	28.19	0.33	-	22.37	28.19	22.75
	N	102	160	44	-	146	160	322

## Discussion

Similar to findings elsewhere, elephants in this study spent most of their time outside BNP, emphasizing the importance of non-protected areas in elephant distribution and range [14, 28]. In the dry season, Doudjatou spent more time in the park, possibly to avoid humans and/or to seek refuge [19], as hunting is prohibited in BNP but allowed in the HC during the dry season. Oldiri's home range was mostly found within the HC, potentially putting her and the herd at greater risk of mortality and trauma associated with losing herd members [29]. However, in spite of potential dangers associated with leaving the park, occurrence inside BNP declined over time, suggesting some benefit to being in high risk areas. This may include the presence of preferred and/or higher quality forage outside BNP, representing a trade-off between better foraging and lower predation risk [30].

Animals may respond to hunting pressure by moving into more protected areas [4] or by avoiding open areas [31] and human activity centers [32, 33]. Indeed, elephants (especially females) avoid human settlements [19, 23, 24, 28]. Aside from direct mortality, negative consequences associated with proximity to human settlements can include behavioural effects like reduced foraging and resting, or increased agitation [34, 35]. In general, the elephants in BNP did not spend a great deal of time in areas near villages. Within approximately 7 km of villages, fewer elephant locations were found with increasing proximity to human settlements. It is important to note, however, that village locations used in analyses represented village *centers*, and that elephant occurrence relative to outlying crop



fields (of which data were unavailable and which largely surround villages) may provide a better idea of HEC with respect to crop raiding in the BWCA.

Quadratic curves of elephant occurrence relative to distance from villages were found in our study and were similar to findings in Burkina Faso [36]. Such relationships may represent the region of the protected area where herds preferred to spend their time. Peaks in occurrence on quadratic curves (generally around 7 to 9 km from villages) may indicate that forage was of superior quality there, that elephants felt safer at this distance, and/or that cover for refuge provided by dense vegetation was greater. Despite an overall low occurrence closer to villages, any elephant presence near human settlements represents potential HEC, particularly during the harvest season, when crop raiding by elephants typically occurs [19]. Indeed, core areas overlapped with villages in HC 2 and 3, which were previously found to have high reports of elephant crop raiding [15]. Expanding farmland around BNP may lead to more frequent interactions between people and elephants [5], and while elephants are not frequent crop raiders, they can cause substantial damage in a single visit, threatening human food security [3, 37].

Several large mammalian species avoid roads due to associated noise and traffic [23, 25, 38-40]. Similarly, Doudjatou never crossed the highway and her occurrence declined with increasing proximity, suggesting that at least for this herd, the highway served as a barrier to movement [41-43], similar to findings elsewhere [23, 25, 44]. Furthermore, several villages occur along the other side of the highway, outside the BNP boundary, including one of the most populated, Gamba (HC 5), with an estimated population size of 2500. This may have contributed to the lack of elephant presence on the other side of the highway. Previous work found that reports of elephant crop raiding were lowest in Gamba relative to villages in HC 2,3, and 7 [15]. In contrast to those villages, smaller species, including baboons, were reported by locals as more frequent crop raiders in Gamba [15].

Elephants differed in their movement relative to unpaved park roads, though overall, most of their locations occurred at greater distances from unpaved park roads, and this did not appear to have any obvious influence on the elephants' use of the BWCA. In contrast, their occurrence increased with proximity to secondary roads, suggesting some benefit to be near such areas, perhaps due to a preference for secondary forest that is typically found near roads, with higher quality forage, and/ or due to the proximity of this road type to the Bénoué River [23, 45, 46]. Several secondary roads are located near this river (Fig. 1), which serves as a primary water source for animals and people during the dry season. Herds may thus be trading off reduced predation risk for access to water and forage found along rivers, particularly during the dry season. Indeed, distance to secondary roads was generally greatest in the late wet season and early dry season (following a period of high rainfall) and smallest near the end of the dry season (following a long period of little to no rainfall). The consistent overlap of core areas with rivers and the elephants' increasing occurrence with proximity to the river illustrate the importance of permanent water sources for savanna elephants, appearing to have the greatest influence on elephant spatial use in the BWCA. The highway's greater distance from the Bénoué River may have also affected the elephants' willingness to venture farther toward the western park region. This dependence on water may further contribute to HEC in the dry season, when water is limited and both species occur close to the Bénoué River [4, 47]. In Tsavo, Kenya, distance to perennial water was the greatest predictor of crop raiding whenever female elephants were involved [48]. This may be similar to the BWCA, where 96% of locals surveyed in the villages of Doudja and Mbaou (HC 2 and 3) reported crop raiding by elephants; these villages were also located close to the Bénoué River [15].

## Implications for conservation

Studies of elephant movement in places facing heavy encroachment from humans are important for understanding HEC and identifying areas important to elephant survival [28]. While elephants in the present study showed individual variation in movement and may not necessarily reflect the entire BNP elephant population, our findings provide insight into how both human and non-human landscape features can affect elephant spatial ecology. For example, the location and importance of perennial water sources for elephants and other wildlife must be considered in future conservation and/or management plans in the BWCA, as elephant movement in the present study appeared strongly linked to the Bénoué River's location, similar to findings elsewhere [24, 36]. The river's proximity to human settlements outside the park may also be influencing the level of HEC in the region. Elephants spent most of their time outside of BNP, thus movement across park boundaries and human interests must be taken into account due to the influence of activity centers on elephants' spatial use [19, 49]. Preventing additional settlement and expansion of crop land can play a major role in reducing HEC, and such activities should at least be prohibited in HC 2 and 3, the areas in the BWCA most frequented by elephants and where reports of crop raiding were previously found to be highest [15]. To our knowledge, movement of only one other elephant in this conservation area has been studied [50]. Therefore, collaring additional elephants in the BWCA should be a priority for future research. This would yield even more understanding about how elephants use the protected area and the impacts of ongoing human disturbance on elephant distribution.

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## References

- [1] Hoare, R. 2000. African elephants and humans in conflict: the outlook for co-existence. *Oryx* 34: 34-38.
- [2] Balmford, A., Moore, J.L., Brooks, T., Burgess, N., Hansen, L.A., Williams, P. and Rahbek, C. 2001. Conservation conflicts across Africa. *Science* 291: 2616-2619.
- [3] Naughton-Treves, L. 1998. Predicting Patterns of Crop Damage by Wildlife around Kibale National Park, Uganda. *Conservation Biology* 12: 156-168.
- [4] Thouless, C.R. 1994. Conflict between humans and elephants on private land in northern Kenya. *Oryx* 28: 119-127.
- [5] Bal, P., Nath, C., Nanaya, K., Kushalappa, C. and Garcia, C. 2011. Elephants also like coffee: Trends and drivers of human–elephant conflicts in coffee agroforestry landscapes of Kodagu, Western Ghats, India. *Environmental Management* 47: 789-801.
- [6] Garcia, C., Marie-Vivien, D., Kushalappa, C.G., Chengappa, P.G. and Nanaya, K.M. 2007. Geographical Indications and Biodiversity in the Western Ghats, India: Can Labeling Benefit

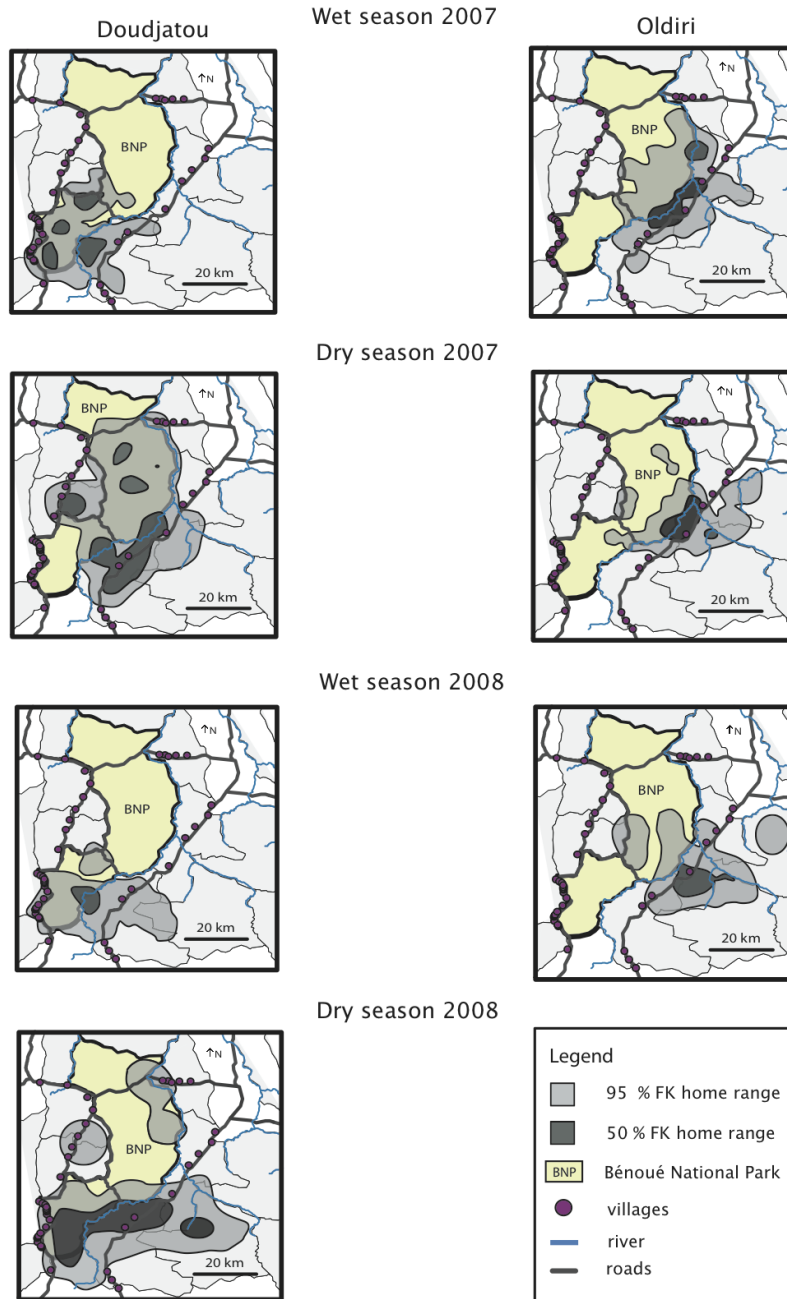


- Producers and the Environment in a Mountain Agroforestry Landscape? *Mountain Research and Development* 27: 206-210.
- [7] Sitati, N.W., Walpole, M.J., Smith, R.J. and Leader-Williams, N. 2003. Predicting spatial aspects of human-elephant conflict. *Journal of Applied Ecology* 40: 667-677.
- [8] Naughton, L., Rose, R. and Treves, A. 1999. *The social dimensions of human-elephant conflict in Africa: a literature review and case studies from Uganda and Cameroon*. Human-Elephant Conflict Task Force, IUCN, Gland, Switzerland.
- [9] Weladji, R.B. and Tchamba, M.N. 2003. Conflict between people and protected areas within the Bénoué Wildlife Conservation Area, North Cameroon. *Oryx* 37: 72-79.
- [10] Blanc, J.J., Barnes, R.F.W., Craig, G.C., Dublin, H.T., Thouless, C.R., Douglas-Hamilton, I. and Hart, J.A. 2007. *African Elephant Status Report 2007: an update from the African Elephant Database*. Occasional paper of the IUCN Species Survival Commission, No. 33, Gland, Switzerland.
- [11] Buij, R., McShea, W.J., Campbell, P., Lee, M.E., Dallmeier, F., Guimondou, S., Mackaga, L. and Guisseougou, N. 2007. Patch-occupancy models indicate human activity as major determinant of forest elephant *Loxodonta cyclotis* seasonal distribution in an industrial corridor in Gabon. *Biological Conservation* 135: 189-201.
- [12] Endamana, D., Sayer, J., Etoga, G. and Bene Bene, L. 2007. Conservation and development: The influence of accessibility, participatory management and immigration around the Bénoué National Park in Cameroon. *Nature and Faune* 22: 10- 20.
- [13] Bouché, P., Douglas-Hamilton, I., Wittemeyer, G., Nianogo, A.J., Doucet, J.L., Lejuene, P. and Vermeulen, C. 2011. Will elephants soon disappear from West African savannahs? *PLoS ONE* 6: 1-11.
- [14] Douglas-Hamilton, I., Krink, T. and Vollrath, F. 2005. Movements and corridors of African elephants in relation to protected areas. *Naturwissenschaften* 92: 158-163.
- [15] Granados, A. and Weladji, R.B. 2012. Human-elephant conflict around Bénoué National Park, Cameroon: Influence on local attitudes and implications for conservation. *Human Dimensions of Wildlife* 17:77-90.
- [16] Boum, R. and Bene Bene, L. 2008. Rapport de suivi des Conflits Populations- Faune autour du Parc National de la Benoue. World Wildlife Fund, Garoua, Cameroon.
- [17] Moss, C.J. 1988. *Elephant Memories: Thirteen Years in the Life of an Elephant Family*. William Morrow, New York, USA.
- [18] Archie, E.A., Moss, C.J. and Alberts, S.C. 2006. The ties that bind: genetic relatedness predicts the fission and fusion of social groups in wild African elephants. *Proceedings of the Royal Society B: Biological Sciences* 273: 513-522.
- [19] Galanti, V., Preatoni, D., Martinoli, A., Wauters, L.A. and Tosi, G. 2006. Space and habitat use of the African elephant in the Tarangire–Manyara ecosystem, Tanzania: Implications for conservation. *Mammalian Biology* 71: 99-114.
- [20] Wittemyer, G., Douglas-Hamilton, I. and Getz, W.M. 2005. The socioecology of elephants analysis of the processes creating multitiered social structures. *Animal Behaviour* 69: 1357-1371.
- [21] SAS. 2008. *The SAS system for Windows*, v. 9.2. SAS Institute Inc. Cary, North Carolina, USA.
- [22] Hooge, P.N. and Eichenlaub, B. 2000. *Animal movement extension to Arcview*. Alaska Science Center - Biological Science Office, U.S. Geological Survey, Anchorage, USA.
- [23] Barnes, R.F.W., Barnes, K.L., Alers, M.P.T. and Blom, A. 1991. Man determines the distribution of elephants in the rain forests of northeastern Gabon. *African Journal of Ecology* 29: 54-63.
- [24] Harris, G.M., Russell, G.J., van Aarde, R.I. and Pimm, S.L. 2008. Rules of habitat use by elephants *Loxodonta africana* in southern Africa: insights for regional management. *Oryx* 42: 66-75.

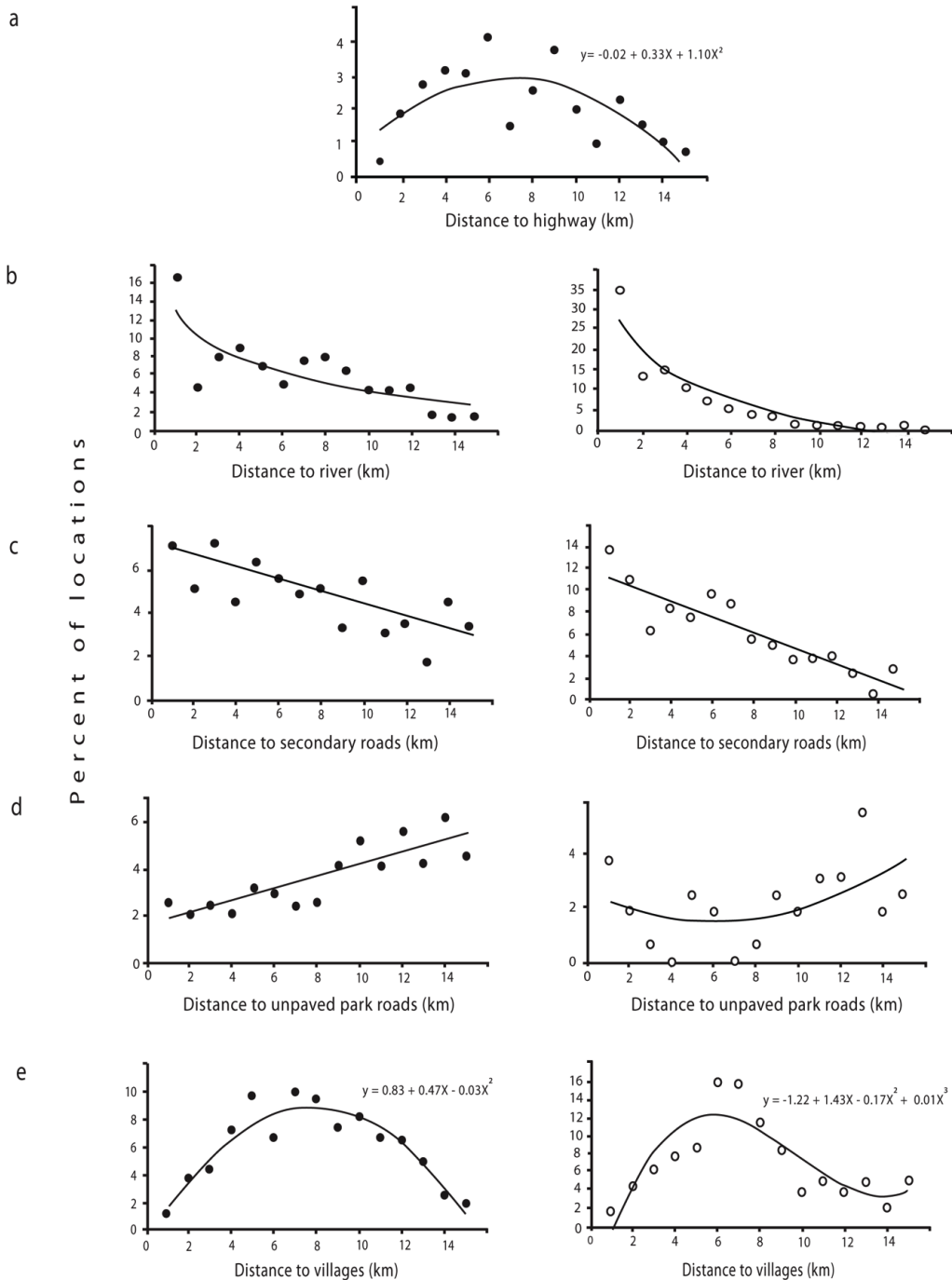
- [25] Newmark, W.D., Boshe, J.I., Sariko, H.I. and Makumbule, G.K. 1996. Effects of a highway on large mammals in Mukumi National Park, Tanzania. *African Journal of Ecology* 34: 15- 31.
- [26] Stokke, S. and du Toit, J.T. 2002. Sexual segregation in habitat use by elephants in Chobe National Park, Botswana. *African Journal of Ecology* 40: 360-371.
- [27] Thouless, C.R. 1995. Long distance movements of elephants in northern Kenya. *African Journal of Ecology* 33: 321-334.
- [28] Graham, M.D., Douglas-Hamilton, I., Adams, W.M. and Lee, P.C. 2009. The movement of African elephants in a human-dominated land-use mosaic. *Animal Conservation* 12: 445-455.
- [29] Bradshaw, G.A., Schore, A.N., Brown, J.L., Poole, J.H. and Moss, C.J. 2005. Elephant breakdown. *Nature* 433: 807.
- [30] Power, R.J. and Compion, S. 2009. Lion predation on elephants in the Savuti, Chobe National Park, Botswana. *African Zoology* 44: 36-44.
- [31] Kilgo, J.C., Labisky, R.F. and Fritzen, D.E. 1998. Influences of hunting on the behavior of white tailed deer: Implications for conservation of the Florida panther. *Conservation Biology* 12: 1359-1364.
- [32] Dorrance, M.J., Savage, P.J. and Huff, D.E. 1975. Effects of snowmobiles on white-tailed deer. *Journal of Wildlife Management* 39: 563-569.
- [33] Rost, G.R. and Bailey, J.A. 1979. Distribution of mule deer and elk in relation to roads. *Journal of Wildlife Management* 43: 634-641.
- [34] Kumar, M.A. and Singh, M. 2011. Behavior of Asian elephant (*Elephas maximus*) in a land-use mosaic: conservation implications for human-elephant coexistence in the Anamalai hills, India. *Wildlife Biology in Practice* 6: 69- 80.
- [35] Ruggiero, R. 1990. The effects of poaching disturbance on elephant behaviour. *Pachyderm* 13: 42-44.
- [36] Hema, E.M., Barnes, R.F.W. and Guenda, W. 2011. Distribution of savannah elephants (*Loxodonta africana africana* Blumenbach 1797) within Nazinga game ranch, Southern Burkina Faso. *African Journal of Ecology* 49: 141-149.
- [37] Okello, M.M. 2005. Land use changes and human-wildlife conflicts in the Amboseli Area, Kenya. *Human Dimensions of Wildlife* 10: 19-28.
- [38] Brody, A.J. and Pelton, M.R. 1989. Effects of roads on black bear movements in western North Carolina. *Wildlife Society Bulletin* 17: 5-10.
- [39] Dyer, S.J., O'Neill, J.P., Wasel, S.M. and Boutin, S. 2002. Quantifying barrier effects of roads and seismic lines on movements of female woodland caribou in northeastern Alberta. *Canadian Journal of Zoology* 80: 839-845.
- [40] Forman, R.T. and Alexander, L.E. 1998. Roads and their major ecological effects. *Annual Review of Ecology and Systematics* 29: 207- 231.
- [41] Jaeger, J.A.G., Bowman, J., Brennan, J., Fahrig, L., Bert, D., Bouchard, J., Charbonneau, N., Frank, K., Gruber, B. and von Toschanowitz, K.T. 2005. Predicting when animal populations are at risk from roads: an interactive model of road avoidance behavior. *Ecological Modelling* 185: 329-348.
- [42] Newmark, W.D. 2008. Isolation of African protected areas. *Frontiers in Ecology and the Environment* 6: 321- 328.
- [43] Trombulak, S.C. and Frissell, C.A. 2000. Review of ecological effects of roads on terrestrial and aquatic communities. *Conservation Biology* 14: 18-30.
- [44] Laurance, W.F., Croes, B.M., Tchignoumba, L., Lahm, S.A., Alonso, A., Lee, M.E., Campbell, P. and Ondzeano, C. 2006. Impacts of roads and hunting on central African rainforest mammals. *Conservation Biology* 20: 1251-1261.

- [45] Gagnon, J.W., Theimer, T.C., Boe, S., Dodd, N.L. and Schweinsburg, R.E. 2007. Traffic volume alters elk distribution and highway crossings in Arizona. *Journal of Wildlife Management* 71: 2318-2323.
- [46] Olivier, R. 1978. *On the ecology of the Asian elephant*. Ph. D. thesis. University of Cambridge. Unpublished, Cambridge, UK.
- [47] Jackson, T.P., Mosojane, S., Ferriera, S.M. and van Aarde, R.J. 2008. Solutions for elephant *Loxodonta africana* crop raiding in northern Botswana: moving away from symptomatic approaches. *Oryx* 42: 83-91.
- [48] Smith, R. and Kasiki, S. 1999. *A spatial analysis of human-elephant conflict in the Tsavo ecosystem*. Kenya IUCN African Elephant Specialist Group Report, Gland, Switzerland.
- [49] Lee, P.C. & Graham, M. 2006. African elephants *Loxodonta africana* and human elephant interactions: implications for conservation. *International Zoo Yearbook* 40: 9-19.
- [50] Foguekem, D., Tchamba, M.N., Macallister, M., Ngassam, P. and Loomis, M. 2007. Application of ArcView Animal Movement Analysis Extension as a tool for monitoring elephant movement: preliminary results from northern Cameroon. *Pachyderm* 43: 29-35.

**Appendix 1.** Seasonal and overall Fixed Kernel (FK) home ranges within the Bénoué Wildlife Conservation Area for Doudjatou and Oldiri.



**Appendix 2.** Percent of locations for each elephant (Doudjatou = closed circles; Oldiri= open circles) within 15 km of a) the highway, b) the Bénoué River, c) secondary roads, d) unpaved park roads, and e) villages, for overall locations, with the exception of Figure 3.3a and 3.3d, which depict Doudjatou and Oldiri's pooled dry season occurrence relative to the highway and unpaved park roads, respectively.



**Appendix 3.** Relationship between each elephants' number of locations and distance within 15 km of the highway, secondary roads, unpaved park roads, villages, and the Bénoué River, within seasons. Chi-square ( $\chi^2$ ) statistics are given with P-values in brackets. Letter subscripts with P-values indicate the shape of the relationship observed between the number of locations and distance to the area being tested: p=positive (occurrence increases with proximity); n= negative (occurrence decreases with distance from area); q= quadratic relationship; c= cubic relationship. Symbols with P-values indicate the distance (km) at which the trend is significant: \* = significant at distances > 2 km; † = significant at distances < 14 km. All other tests where P < 0.05, were significant at  $\leq$  15 km relative to the area of interest. Df=1 for each test.

Year Season	2007		2008		Both years		All locations
	Wet	Dry	Wet	Dry	Wet	Dry	
<i>Doudjatou</i>							
Highway	0.30 (0.586)	6.80 (0.009 <sup>q</sup> )	13.44 (<0.001 <sup>p*</sup> )	3.46 (0.063 <sup>q</sup> )	2.53 (0.112)	17.11 (<0.001 <sup>q</sup> )	0.05 (0.821)
Secondary roads	0.58 (0.441)	24.67 (<0.001 <sup>n</sup> )	7.86 (0.005 <sup>n*</sup> )	0.07 (0.791)	2.18 (0.140)	8.77 (0.003 <sup>n</sup> )	7.69 (0.006 <sup>n</sup> )
Unpaved park roads	12.72 (<0.001 <sup>q</sup> )	4.97 (0.026 <sup>p*</sup> )	30.38 (<0.001 <sup>p</sup> )	7.13 (0.008 <sup>p</sup> )	11.49 (<0.001 <sup>p</sup> )	9.34 (0.002 <sup>q</sup> )	10.78 (0.001 <sup>p</sup> )
Villages	5.88 (0.015 <sup>p*</sup> )	27.33 (<0.001 <sup>q</sup> )	4.31 (0.038 <sup>p</sup> )	23.68 (<0.001 <sup>q</sup> )	12.76 (<0.001 <sup>q</sup> )	5.65 (0.018 <sup>q</sup> )	39.04 (<0.001 <sup>q</sup> )
River	6.25 (0.012 <sup>q</sup> )	12.89 (<0.001 <sup>n</sup> )	21.39 (<0.001 <sup>n</sup> )	20.05 (<0.001 <sup>n</sup> )	15.13 (<0.001 <sup>n</sup> )	30.17 (<0.001 <sup>n</sup> )	42.24 (<0.001 <sup>n</sup> )
<i>Oldiri</i>							
Secondary roads	19.61 (<0.001 <sup>n</sup> )	19.81 (<0.001 <sup>n</sup> )	1.89 (0.170)	-	8.49 (0.004 <sup>n</sup> )	19.81 (<0.001 <sup>n</sup> )	17.59 (<0.001 <sup>n</sup> )
Unpaved park roads	0.94 (0.333)	16.60 (<0.001 <sup>q</sup> )	3.64 (0.056 <sup>q</sup> )	-	1.18 (0.277)	16.60 (<0.001 <sup>q</sup> )	2.56 (0.110)
Villages	8.34 (0.004 <sup>q</sup> )	11.29 (<0.001 <sup>q</sup> )	6.65 (0.001 <sup>c</sup> )	-	6.97 (0.008 <sup>q</sup> )	11.29 (<0.001 <sup>q</sup> )	6.93 (0.009 <sup>c</sup> )
River	65.62 (<0.001 <sup>n</sup> )	126.65 (<0.001 <sup>n</sup> )	11.92 (<0.001 <sup>n</sup> )	-	42.33 (<0.001 <sup>n</sup> )	126.05 (<0.001 <sup>n</sup> )	75.64 (<0.001 <sup>n</sup> )