African Journal of Ecology

Censusing large mammals in Kibale National Park: evaluation of the intensity of sampling required to determine change

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Abstract

Monitoring programmes are essential for management of large mammal populations because they can detect population change. It is vital that we have the means to evaluate the effectiveness of protected areas. Kibale National Park is a stronghold for large mammal conservation in Uganda. Past wildlife surveys in Kibale focused on specific taxa or areas, but our large mammal survey covered the entire protected area and we evaluated the intensity of sampling required to determine population change. Using line transect sampling, we found that the distribution of large mammals was nonrandom and related to habitat-type. However, confidence intervals of population estimates revealed that much more intensive sampling was required to detect changes in population density at a time scale reasonable for management. For many species, populations would have to decline by 40–60% for this method to detect population change. Post-stratification decreased confidence intervals of density estimates slightly, increasing our ability to detect change. However, confidence intervals of estimates were still too large to detect a meaningful population change on a time scale that would allow management to take action. Most incidences of illegal activity were about 5 km from the park boundary; however, animal densities were not lower in this area.

Key words: large mammals, population estimation, primates, survey

Résumé

Les programmes de suivi sont essentiels pour la gestion de populations de grands mammifères parce qu'ils permettent de détecter tout changement de population. Il est vital que nous ayons les moyens d'évaluer l'efficacité des aires protégées. Le Parc National de Kibale est un haut-lieu de la conservation des grands mammifères en Ouganda. Des études antérieures faites sur la faune sauvage à Kibale se sont focalisées sur des taxons ou des sites spécifiques, mais notre étude de grands mammifères a couvert la totalité de l'aire protégée et nous avons évalué quelle était l'intensité d'échantillonnage nécessaire pour déterminer un changement de population. En recourant à l'échantillonnage par transect linéaire, nous avons trouvé que la distribution des grands mammifères n'était pas aléatoire et qu'elle était liée au type d'habitat. Cependant, les intervalles de confiance des estimations de population ont révélé qu'il était nécessaire de faire des échantillonnages beaucoup plus intenses pour déceler des changements de population dans des délais raisonnables pour la gestion. En effet, pour de nombreuses espèces, il faudrait que les populations déclinent de 40–60% pour que cette méthode détecte un changement de population. La post-stratification diminuait légèrement les intervalles de confiance des estimations de densité, et augmentait notre capacité de déceler un changement. Pourtant, les intervalles de confiance des estimations étaient encore trop grands pour détecter un changement de population significatif dans un délai qui permette à la gestion de prendre des mesures. La plupart des cas d'activités illégales se passaient à moins de cinq kilomètres de la limite du parc, et pourtant la densité des animaux n'était pas moindre dans cette zone-là.

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Introduction

Monitoring wildlife populations and habitats is an important way to assess the impacts of human actions on nature and understand the natural rates of wildlife changes (Balmford, Green & Jenkins, 2003). A systematic analysis of population trends and habitats is needed to mitigate the decline of biodiversity and document extinction rates (Balmford, Green & Jenkins, 2003; Kühl *et al.*, 2008). Survey and monitoring programmes permit evaluation of the sources and impacts of potential threats including: habitat degradation and fragmentation, poaching and natural catastrophes, such as hurricanes, fires and disease (Kühl *et al.*, 2008). Globally, tropical forests account for nearly 50% of all known species (NRC, 1992); however, the futures of these highly diverse ecosystems are threatened by escalating rates of forest conversion and degradation (Brown & Lugo, 1990; FAO, 2005; Chapman, Lawes & Eeley, 2006). The primary mechanism for protecting this diversity is through the establishment of wildlife protected areas (Oates, 1999; Terborgh *et al.*, 2002). However, less than 5% of tropical forests are protected from human exploitation, and many of these legally protected areas are still subjected to illegal human activities (Peres, 1990; Oates, 1996) or dramatic population declines caused other factors such as disease outbreaks (e.g. declines in gorilla populations from Ebola; Huijbergts & Wachter, 2003; Walsh *et al.*, 2003). Accordingly, wildlife monitoring is critical in developing plans for protected area management and the surrounding areas (Kremen, Merenlender & Murphy, 1994).

Kibale National Park is a stronghold for large mammals within Uganda and has been protected by the Uganda Wildlife Authority since 1993. While multiple censuses have been conducted in Kibale, they were typically localized (with the exception of an early elephant survey; Wing & Buss, 1970) and focused on specific taxa (Skorupa, 1988; Chapman *et al.*, 2000, in press; Plumptre & Cox, 2006). We designed a line transect survey to provide a large-scale evaluation of the large mammal distribution within the park that was appropriate for the use of the analytical procedures of the DISTANCE software. Protected area managers have the task of responding to declines in wildlife populations that have been identified during monitoring but if managers are to be able to respond, they must be sure that survey methods are adequate to detect change (Plumptre, 2000).

The objectives of our research were twofold: first, we aimed to estimate of the population size of the large mammals in Kibale National Park, Uganda using line transect methodology. Second, we sought to evaluate the results of these estimations to assess the magnitude of change needed for this type of method to detect an important population change.

Materials and methods

Study site

Kibale National Park, Uganda covers 795 km^2 (0 13′–0 41′N and 30 19′–30 32′E) and ranges in elevation from 1590 m in the north to 1110 m in the south (Howard, 1991; Struhsaker, 1997; Chapman & Lambert, 2000; Lwanga, Butynski & Struhsaker, 2000). The area was gazetted as a Forest Reserve in 1932, and became a National Park in 1993 (Struhsaker, 1997). The most extensive habitats in Kibale National Park are forest (57.9%) and grassland (14.6%; Fig. 1). Grasslands are much more common in the southern part of the park than in the northern areas (Chapman & Lambert, 2000), resulting from the drier climate in the south and forest clearing that occurred in the 1970s and 1980s when the southern area was not effectively protected. Fauna include threatened and near threatened species such as *Loxodonta africana* (elephants), *Panthera pardus* (leopard), *Pan troglodytes* (chimpanzee) and *Procolobus rufomitratus* (red colobus monkeys). Prominent are the thirteen species of nonhuman primates (67% of the country's total species).

Survey design

We focused on large mammals, including primates, using direct observations along precut line transects. We used DISTANCE (Version 5.0 1998–2009) to estimate population density and calculated the 95% confidence interval around these estimates (Burnham, Anderson & Laake, 1980; Buckland *et al.*, 1993; Laake *et al.*, 1994; Burnham, Plumptre & Cox, 2006). We placed 40 evenly spaced 4 km transects every 2.8 km throughout the park (Fig. 2). After identifying the starting point of each transect, we cut trails in a north–south orientation, checking direction every 250 m. Transects were cut a minimum of 3 weeks before any data was collected. However, as the field staff could not access all transects because of topographic variation

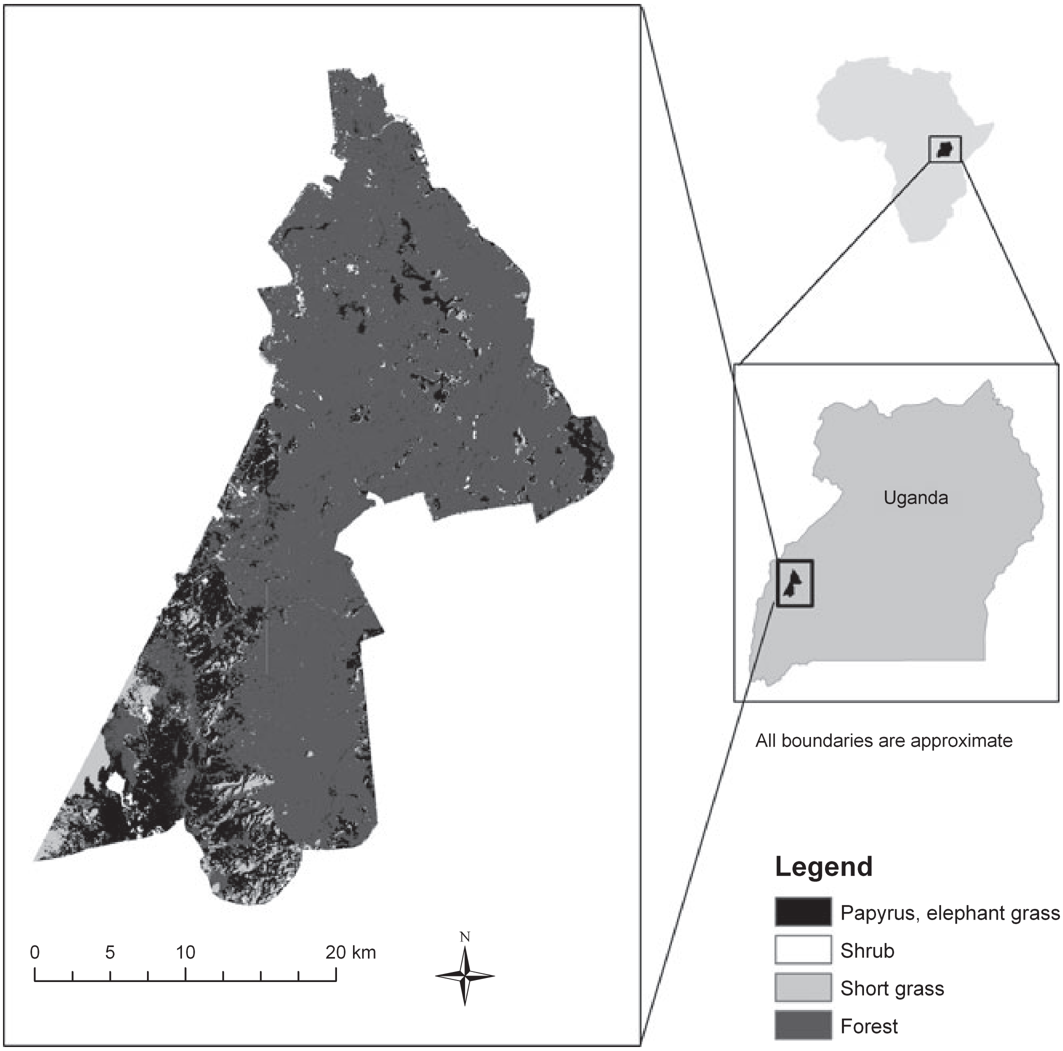

Fig 1 The vegetation patterns found in Kibale National Park, Uganda and the location of the park

(i.e. swamps and rivers), only 37 out of the 40 transects were completed. Primates, elephant and sitatunga (*Tragelaphus spekei*) may have been using these swamps to some extent and thus their density may be underrepresented in these areas. We attempted to sample transects every 20 days, but the sampling interval ranged from 18 to 23 days (mean = 20.6 days) because of logistic constraints (e.g. transport difficulties or rain).

Because of the forested nature of many areas within Kibale and the fact that many species avoided human observers, we used indirect census methods for some species (dung for elephants, buffalos (*Syncerus caffer*), bush pigs (*Potomochoerus porcus*), and nests for chimpanzees. Chimpanzees rarely use the same nest more than once, and we considered nest-builders to be weaned individuals (Plumptre & Cox, 2006). To do this, we visited each transect three times, to undertake a dung and marked nest per dung count (Plumptre *et al.*, 2001; Plumptre & Cox, 2006). Repeated visits avoided the need to calculate decay rates for both nests and dung (Plumptre *et al.*, 2001). The interval between resampling of the same transect was short enough that a dung sample or a chimpanzee nest constructed just after a transect was sampled would not have decayed by the next time the transect was sampled (Wing & Buss, 1970; Plumptre & Harris, 1995; Plumptre *et al.*, 2001).

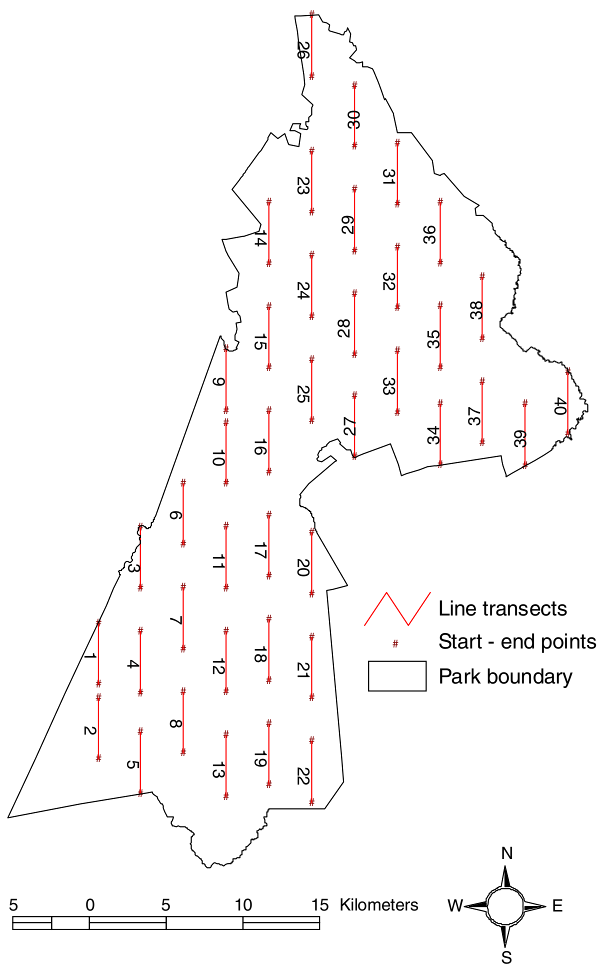

Fig 2 Map of Kibale National Park, Uganda showing the location of the ground census transects

Data collection

We conducted censuses between 25 August 2005 and 8 November 2005 for a total of 61 census days. Four census teams of four people, each headed by an individual knowledgeable in using line transect sampling, walked transects between 0630 and 0930 hours. Each group collected data on one transect per day. After reaching the starting point for each transect, the census crew quietly walked the already established transect line at approximately 1 km h^{-1} as suggested by previous authorities (Struhsaker, 1975; National Research Council, 1981). We counted each large mammal or group of large mammals and, while there is controversy on how to census primates (Chapman, Fedigan & Fedigan, 1988; Mitani, Struhsaker & Lwanga, 2000; Plumptre & Cox, 2006; Teelen, 2007; Hassel-Finnegan *et al.*, 2008; Marshall, Lovett & White, 2008), we followed the recommendation used by the DISTANCE sampling approach (Laake *et al.*, 1994). Accordingly, we recorded the perpendicular distance from the observation to the centerline of the transect using a tape measure and range finder (Model: RANGING 400). We also recorded illegal activities whenever they were encountered.

Animal sightings and analysis

We counted all chimpanzee nests encountered and scored them according to their age (fresh, dry or very old), identified monkey groups by species, counted the piles of large mammal dung and recorded sightings of large mammals. The interval between censuses was shorter than the time that animal signs would disappear, and the entire duration between first and last census was only 100 days. To estimate animal density, we divided the observed number of dung piles by the estimated dung production rate per day (17 per day elephants, Wing & Buss, 1970; 5.1 per day buffalo, Plumptre & Harris, 1995; 7 per day bush pig, Plumptre & Harris, 1995). Similarly, we divided the number of chimpanzee nests by the estimated nest production rate per day of nest buildings (1.1, which accounts for dependent offspring who do not make their own nests; Plumptre & Reynolds, 1997).

We analyzed all the census data using DISTANCE software (Laake *et al.*, 1994), and we made the following assumptions: (i) we identified all animals per dung per nests accurately; (ii) we detected all animals on or very close to the centre line of the transect; (iii) animal observations were independent of each other (i.e., detection of one observation did not affect detection of another observation); and (iv) we detected all animals at their initial positions when first sighted. In addition, DISTANCE analysis requires at least 60 observations per species to accurately estimate density (Buckland *et al.*, 1993).

Results

We calculated the population estimates and their associated 95% confidence intervals for each species (Table 1). The density of these species was not homogenously distributed; clustering of some species occurred in particular areas and habitats (Fig. 3). Although we used nests and dung to estimate densities of chimpanzees and elephants, we encountered thirteen chimpanzee parties and five

Table 1 Population estimates (# per km^2) for select mammals in Kibale National Park, Uganda. Primate densities are reported as groups per km^2. Elephant, buffalo and bush pig density data are based on individual dung counts and estimates of defecation rate (17 per day elephants, Wing & Buss, 1970; 5.1 per day day buffalo, Plumptre & Harris, 1995; 7 per day bush pig, Plumptre & Harris, 1995). Chimpanzee density is calculated based on nest counts (we divided the number of chimpanzee nests by the estimated nest production rate per day of nest buildings, 1.1, which accounts for dependent offspring who do not make their own nests; Plumptre & Reynolds, 1997)

Species	Clusters	Individuals	Density	SE	95% Confidence		Pop size	SE	95% Confidence	
					Lower CL	Upper CL			Lower CL	Upper CL
Black and white colobus (*Colobus guereza*)	72	415	13.1	2.6	8.9	19.2	7346	1432	5009	10,773
Grey-cheeked mangabeys (*Lophocebus albigena*)	92	786	20.7	4.1	14	30.6	11,603	2283	7848	17,153
Red colobus (*Procolobus rufomitratus*)	127	2118	54	8.9	39	74.7	30,218	4974	21,815	41,857
Red tailed monkeys (*Cercopithecus ascanius*)	226	1990	66.6	10	49.4	89.8	37,312	5603	27,676	50,301
Baboons (*Papio anubis*)	37	523	11.6	3.7	6.2	21.6	6468	2096	3451	12,121
Elephants (*Loxodonta africana*)	1128	1175	0.5	0.1	0.3	0.9	393	107	230	675
Chimpanzee nests (*Pan troglodytes*)	841	865	1.2	0.3	0.7	1.7	921	201	544	1375
Buffalo (*Syncerus caffer*)	78	84	0.7	0.3	0.4	1.4	554	195	280	1098
Bush pig (*Potomochoerus porcus*)	69	83	0.7	0.2	0.4	1.3	556	172	305	1016

groups of elephants during the survey. We encountered other species during the survey, but sightings were uncommon and did not meet DISTANCE's sample size criteria. These included blue monkeys (*Cercopithecus mitis*, fourteen groups), Uganda kob (*Kobus kob*, twelve clusters), L'hoesti monkey (*Cercopithecus lhoesti*, ten groups), red duiker (*Cephalophus harveyi*, fourteen clusters), blue duiker (*Cephalophus moniticola*, nine clusters), bush buck (*Tragelaphus,* five individuals), sitatunga (*Tragelaphus spekei*, one cluster) and Hippopotamus (*Hippopotamus amphibius*, one cluster). We did not see three large mammals that occur in Kibale: the giant forest hog (*Hylochoerus meinertzhageni*), leopard (*Panthera pardus)* and golden cat (*Profelis aurata* see Aronsen, 2009 for camera trap data on the present of golden cat in Kibale).

We encountered 77 signs of illegal activities. The majority of the incidences we encountered were pole cutting, which accounted for 65% of all records of illegal activities. This activity was found throughout the park, but was concentrated in an area where pines, planted when the area was a forest reserve, had recently been removed. Only 12% of the incidences we observed involved pitsawing of larger trees; these were generally concentrated in the north of the park. We found two incidences of pit traps, which are large pits constructed with the intent that large animals will fall into the pit while running and be captured. One of these pits was to the far north near the park boundary, and one was in the interior of the park approximately at the middle of its north-south axis. Snares, likely set for duikers and bushbuck, involved 7.8% of the incidence of illegal activities and they were distributed throughout the park, but were generally found relatively near the park's boundary. We noted nine instances of cattle grazing, primarily in the south of the park, and we noted one case of bush burning; again in the south of the park. In general, with the exception of the pole cutting near the former pine plantation, most incidences of illegal activity were within approximately 5 km of the park's boundary.

Discussion

Many censuses have been carried out in Kibale. However, this is the first survey to consider all large mammals in the entire protected area. Population sizes obtained by Plumptre *et al.* (2001) and Chapman *et al.* (2000, 2002) and Mitani, Struhsaker & Lwanga (2000) were on an average higher than those found here, particularly with respect to primates; however, these studies selected sites with specific logging histories and forest types. Consequently, this does not permit useful comparisons with our survey. Additionally, these surveys used different methods prohibiting direct comparisons (excluding Plumptre *et al.*, 2001). However, although the study design precludes direct comparisons, these prior surveys provide important information on how primates and elephants use colonizing, successional and old growth forest (Struhsaker, Lwanga & Kasenene, 1996; Chapman *et al.*, 2000; Mitani, Struhsaker & Lwanga, 2000; Lwanga, 2003, 2006; Lawes & Chapman, 2005) and allow for tentative predictions of how populations will respond to future forest regeneration. To monitor change over time, we need to survey the same areas using identical methods. To facilitate this, the Ugandan Wildlife Authority has retained the exact GPS locations of each transect permitting replication (Wanyama, 2005).

Our monitoring concentrated on nine of the most common mammals, as these were the species that met the sample size needed for the use of the analytical DISTANCE program. Six of these species were primates. Redtail monkeys (*Cercopithecus ascanius*) and mangabeys (*Lophocebus albigena*) were found throughout the park, and their highest density occurred in the south and central regions. Baboons (*Papio anubis*) were found in both forest, grassland and Acacia-grassland areas. They were most common in the central and southern regions of the park, and long-term researchers have observed that their populations seem to be slowly expanding to the north (C.A. Chapman, unpublished data). We found the black-and-white colobus (*Colobus guereza*) and red colobus throughout the forested areas of park with a fair amount of spatial variance between areas in their abundance (see also Chapman *et al.*, 2002). While we found chimpanzees throughout most of the park, we did not find them in the grasslands to the far south; they were most abundant in the central and southern forests that are in close proximity to the Dura River. We observed the highest densities of elephants in the eastern and central parts of the park; both areas are comprised mainly of forest and grassland. We found that buffalo were most common in the southern and central areas of the park. This increase in density to the south where Kibale connects to Queen Elizabeth National Park may indicate that there is movement between the two parks. Lastly, we found bush pigs throughout the park with the exception of the very southwest grassland area of the park. Most incidences of illegal activity were within approximately 5 km of the park's boundary, with the exception of the pole cutting near the former pine plantation. However, in general there was no strong evidence that animal densities were lower in this boundary area.

The merit of monitoring wildlife populations is clear because monitoring enables protected area managers to detect population changes and extinction rates (Caughley, 1994), but in developing countries such as Uganda where resources are limited, monitoring is carried out at the expense of other activities that are often of immediate concern (e.g. patrolling and prevention of poaching, community outreach). As a result, careful thought must be placed on how financial resources should be distributed and the value of repeating a survey of this scale. Thus, we ask what sort of wildlife declines would have had to occur to detect change using this census method. The data here had coefficient's of variation (CV) ranging between 14% and 35% (see Plumptre, 2000 for this calculation). To detect a population change and be confident of its significance at the 5% level, we would on average need to have a 38–97% change. If we can accept significance at the 20% level then we would need between 18% and 45% in population change (Plumptre, 2000). Given the difficulty of convincing government agencies of the need to expend scarce resources in monitoring, it is probable that only after a significant decline was identified that action would be taken and resources allocated (Mooers *et al.*, 2007). For example, if low intensity monitoring documented a 60% decline in Kibale chimpanzee population, one of the largest in East Africa, this would probably be too severe and too late to initiate effective conservation.

One way to reduce the large 95% confidence intervals would be to stratify the sample by habitat (Plumptre, 2000). For example, to examine changes in chimpanzee density, more transects could be placed in areas where chimpanzee nest density is high and fewer placed where nest densities are low, and none in habitats that are not occupied by chimpanzees. The limitation of this method is that the same stratification is unlikely to simultaneously work for a number of different species. In addition, high-density areas may be the safest or the most preferred habitats and thus the last to show change (Plumptre, 2000). For example, as the population generally declined, animals in less preferred habitats could move into the preferred habitat and one may only detect a population change when the less preferred habitats no longer supported the target species (Rakitin & Kramer, 1996). However, it is possible to post-stratify data using DISTANCE. We post-stratified the data using this method for chimpanzee nests and red-tailed monkeys by stratifying

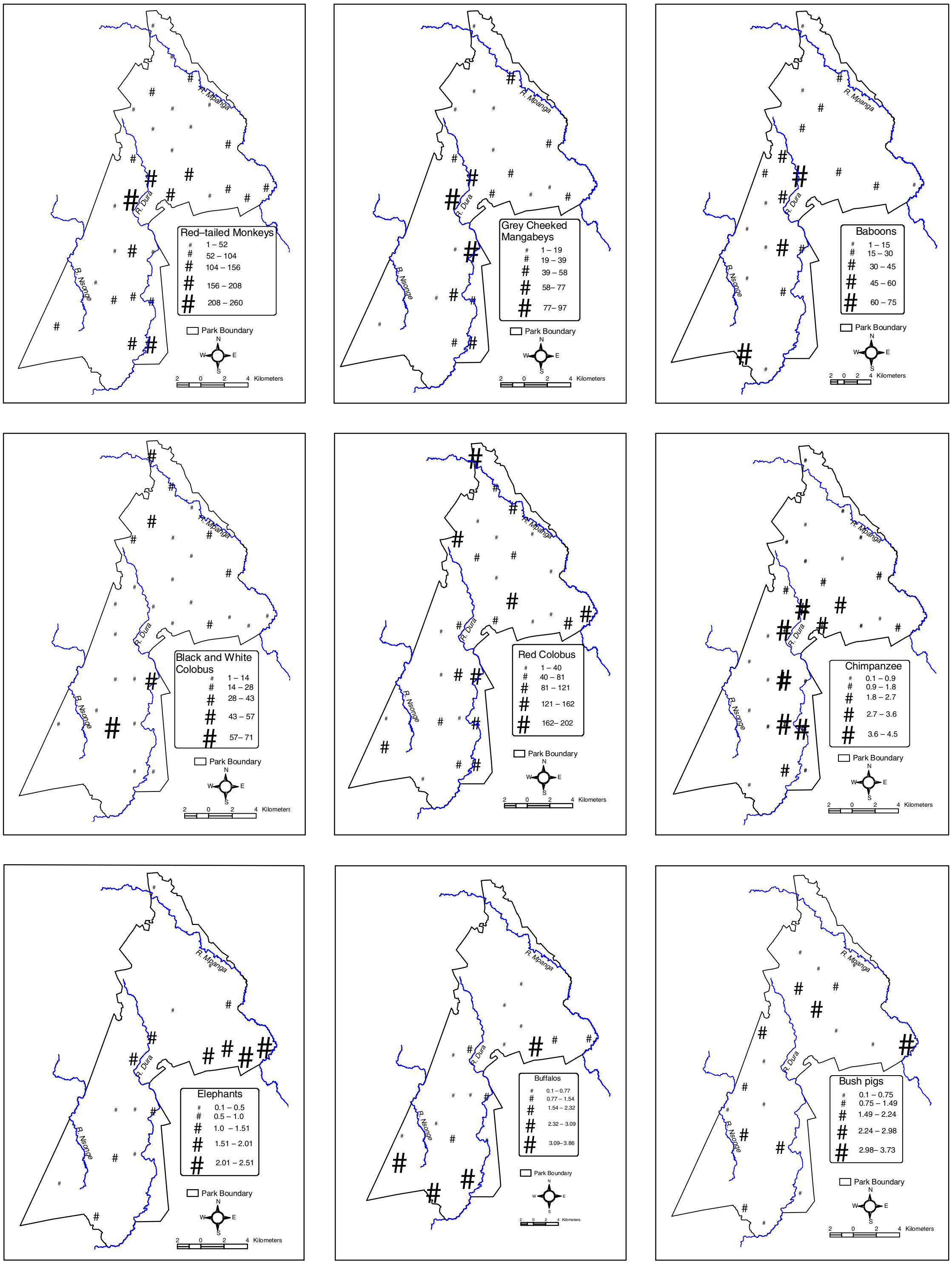

Fig 3 Spatial distribution of mammals found along the transects in Kibale National Park, Uganda. The size of the symbol is proportional to the density along that transect at that site

transects into high, medium and low density areas. We found that stratification improved the CV of the density estimate by 1–3% and thus only slightly increased the ability to detect a significant population change (Table 2).

Our research suggests that the conservation managers should consider accepting greater uncertainty in their estimation of population change estimates if they are to act before a major loss of species has occurred or to invest much more effort in monitoring and increase sampling effort. If we accept a significant change at $P = 0.20$, we will be able to detect change in Kibale of about 18–23% in the population with post-stratification. The level at which managers should accept that a significant change has occurred is open to debate and further study. We also suggest that ancillary data be collected to support estimations of population declines. For instance, patrols should record signs of carcasses and changes in sighting frequency during patrols. Furthermore, given the scarcity of conservation funding, it is desirable to evaluate the effort invested into a census relative to its accuracy and costs. Our census teams included four groups of four people and two support staff per group to handle the logistics of feeding and accommodation. The total cost of the census was approximately $12,500 U.S. dollars, which did not include the cost of outfitting the teams or transport to the sites.

The fact that many tropical mammals are increasingly threatened and isolated within national parks and parks are often subject to illegal activities emphasizes the need for population estimates. It is also clear that conservation biologists need a better understanding how to design and implement surveys to obtain accurate estimates of population change on a time frame whereby managers can adequately respond.

Table 2 Comparison of group density (red-tailed monkey) and individual density (chimpanzee) estimates with and without post-stratification for two primate species. The CV and percentage change in population that could be detected at a 5% probability ($P = 0.05$) and 20% probability ($P = 0.20$) are given

Measure	Chimpanzee	Red-tailed monkey
No stratification		
Density	1.2	66.6
% CV	21.8	15.0
5% Probability	60.3	41.6
20% Probability	28.1	19.4
With post-stratification		
Density	1.1	58.4
% CV	17.7	14.1
5% Probability	49.1	39.0
20% Probability	22.9	18.1

Acknowledgements

Uganda Wildlife Authority undertook this survey of large mammals in Kibale National Park in collaboration with the Wildlife Conservation Society. We would like to thank Nabert Mutungire, Moses Gonya, Timothy Akuguzibwe and Richard Kusemererwa who participated in the surveys with UWA rangers. Joel Hartter from the University of New Hampshire made Fig. 1. Funding was provided by The Daniel K. Thorne Foundation, the John D. and Catherine T. MacArthur Foundation, the Uganda Wildlife Authority and the Wildlife Conservation Society. We thank two anonymous reviewers for very detailed and helpful comments on the submitted manuscript.

References

Aronsen, G.P. (2009) *New Photographic Evidence of the African Golden Cat (Profelis aurata Temminck) Afr. J. Ecol*, doi: 10.1111/j.1365-2028.2009.01117.x.

Balmford, A., Green, R.E. & Jenkins, M. (2003) Measuring the changing state of nature. *Trends Ecol. Evol.* **18,** 326–330.

Brown, S. & Lugo, A.E. (1990) Tropical secondary forest. *J. Trop. Ecol.* **6,** 1–32.

Buckland, S.T., Anderson, D.R., Burnham, K.P. & Laake, J.L. (1993) *Distance Sampling: Estimating Abundance of Biological Populations*. Chapman & Hall, London.

Burnham, K.P., Anderson, D.R. & Laake, J.L. (1980) Estimation of density from line-transect sampling of biological populations. *Wildlife Monogr.* **71,** 7–202.

Caughley, G. (1994) Directions in conservation biology. *J. Anim. Ecol.* **63,** 215–244.

Chapman, C.A., Fedigan, L.M. & Fedigan, L. (1988) A comparison of transect methods of estimating population densities of Costa Rican primates. *Brenesia* **30,** 97–80.

Chapman, C.A. & Lambert, J.E. (2000) Habitat alteration and the conservation of African primates: case study of Kibale National Park, Uganda. *Am. J. Primatol.* **50,** 169–185.

Chapman, C.A., Lawes, M.J. & Eeley, H.A.C. (2006) What hope for African primate diversity? *Afr. J. Ecol.* **44,** 1–18.

Chapman, C.A., Balcomb, S.R., Gillespie, T., Skorupa, J. & Struhsaker, T.T. (2000) Long-term effects of logging on African primate communities: a 28 year comparison from Kibale National Park, Uganda. *Conserv. Biol.* **14,** 207–217.

Chapman, C.A., Chapman, L.J., Bjorndal, K.A. & Onderdonk, D.A. (2002) Application of protein to fiber ratios to predict colobine abundance on different spatial scales. *Int. J. Primatol.* **23,** 283–310.

Chapman, C.A., Struhsaker, T.T., Skorupa, J.P., Snaith, T.V. & Rothman, J.M. (in press) Understanding long-term primate community dynamics: implications of forest change. *Ecol. Appl.*

Fao (2005) *Global Forest Resources Assessment 2005: Progress Towards Sustainable Forest Management*. FAO Forestry Paper 147, Rome.

Hassel-Finnegan, H., Borries, C., Larney, E., Umponjan, M. & Koenig, A. (2008) How reliable are density estimates for diurnal primates? *Int. J. Primatol.* **29,** 1175–1187.

Howard, P.C. (1991) *Nature Conservation in Uganda's Tropical Forest Reserves*. IUCN, Gland.

Huijbergts, D. & Wachter, D.P. (2003) Ebola and the decline of gorilla (*Gorilla gorilla*) and chimpanzee (*Pan troglodytes*) populations in the Minkebe Forest, north-eastern Gabon. *Oryx* **37,** 437–443.

Kremen, C., Merenlender, A.M. & Murphy, D.D. (1994) Ecological monitoring: a vital need for integrated conservation and development program in the tropics. *Conserv. Biol.* **8,** 388–397.

Kühl, H., Maisels, F., Ancerenaz, M. & Williamson, E.A. (2008) *Best Practice Guidelines for Surveys and Monitoring of Great Ape Populations*. IUCN, Gland.

Laake, J.L., Buckland, S.T., Anderson, D.R. & Burnham, K.B. (1994) *Distance User's Guide*. Colorado Cooperative Fishes and Wildlife Unit, Colorado State University, Fort Collins.

Lawes, M.J. & Chapman, C.A. (2005) Does the herb *Acanthus pubescens* and/or elephants suppress tree regeneration in disturbed Afrotropical forests? *For. Ecol. Manage.* **221,** 274–284.

Lwanga, J.S. (2003) Forest succession in Kibale National Park, Uganda: implications for forest restoration and management. *Afr. J. Ecol.* **41,** 9–22.

Lwanga, J.S. (2006) Spatial distribution of primates in a mosaic of colonizing and old growth forest at Ngogo, Kibale National Park, Uganda. *Primates* **47,** 230–238.

Lwanga, J.S., Butynski, T.M. & Struhsaker, T.T. (2000) Tree population dynamics in Kibale National Park, Uganda 1975–1998. *Afr. J. Ecol.* **38,** 238–247.

Marshall, A.R., Lovett, J.C. & White, P.C.L. (2008) Selection of line-transect methods for estimating the density of group-living animals: lessons from the primates. *Am. J. Primatol.* **70,** 452–462.

Mitani, J.C., Struhsaker, T.T. & Lwanga, J.S. (2000) Primate community dynamics in old growth forest over 23.5 years at Ngogo, Kibale National Park, Uganda: Implications for conservation and census methods. *Int. J. Primatol.* **21,** 269–286.

Mooers, A.O., Prugh, L.R., Festa-Bianchet, M. & Hutchings, J.A. (2007) Biases in legal listings under Canadian Endangered Species legislation. *Conserv. Biol.* **21,** 572–575.

National Research Council (1981) *Techniques for the Study of Primate Population Ecology*. National Academy Press, Washington.

National Research Council (1992) *Conserving Biodiversity: A Research Agenda for Development Agencies*. National Academy Press, Washington, D.C.

Oates, J.F. (1996) Habitat alteration, hunting, and the conservation of folivorous primates in African forests. *Aust. J. Ecol.* **21,** 1–9.

Oates, J.F. (1999) *Myth and Reality in the Rain Forest*. University of California Press, Berkeley.

Peres, C.A. (1990) Effects of hunting on western Amazonian primate communities. *Biol. Conserv.* **54,** 47–59.

Plumptre, A.J. (2000) Monitoring mammal populations with line transect techniques in African forests. *J. Appl. Ecol.* **37,** 356–368.

Plumptre, A.J. & Cox, D. (2006) Counting primates for conservation: primate survey in Uganda. *Primates* **47,** 65–73.

Plumptre, A.J. & Harris, S. (1995) Estimating the biomass of large mammalian herbivores in a tropical montane forest: a method of faecal counting that avoid assuming 'steady state' system. *J. Appl. Ecol.* **32,** 111–120.

Plumptre, A.J. & Reynolds, V. (1997) Nesting behavior of chimpanzees: Implications for censuses. *Int. J. Primatol.* **18,** 475–485.

Plumptre, A.J., Mugume, S., Cox, D. & Montgomery, C. (2001) *Chimpanzee and Large Mammal Surveys of Budongo Forest Reserve and Kibale National Park*. Unpublished report to the Wildlife Conservation Society, New York, NY, USA.

Rakitin, A. & Kramer, D.L. (1996) Effect of a marine reserve on the distribution of coral reef fishes in Barbados. *Mar. Ecol. Prog. Ser.* **131,** 9–113.

Skorupa, J.P. (1988) *The Effect of Selective Timber Harvesting on Rain Forest Primates in Kibale Forest, Uganda*, PhD Thesis. University of California, Davis.

Struhsaker, T.T. (1975) *The Red Colobus Monkey*. University of Chicago Press, Chicago.

Struhsaker, T.T. (1997) *Ecology of an African Rain Forest: Logging in Kibale and the Conflict Between Conservation and Exploitation*. University of Florida Press, Gainesville.

Struhsaker, T.T., Lwanga, J.S. & Kasenene, J.M. (1996) Elephants, selective logging, and forest regeneration in the Kibale Forest, Uganda. *J. Trop. Ecol.* **12,** 45–64.

Teelen, S. (2007) Primate abundance along five transect lines at Ngogo, Kibale National Park, Uganda. *Am. J. Primatol.* **69,** 1–15.

Terborgh, J., Van Schaik, C.P., Davenport, L. & Rao, M. (2002) *Making Parks Work: Strategies for Preserving Tropical Nature*. Island Press, New York.

Walsh, T.D., Abernethy, K.A., Bermejo, M., Beyers, R., De Wachter, P., Akou, M.E., Huijbregts, B., Mambounga, D.I., Toham, A.K., Kilbourn, A.M., Lahm, S.A., Latour, S., Maisels, F., Mbina, C., Mihindou, Y., Oblang, S.N., Effa, E.N., Starkey, M.P., Telfer, P., Thiboult, M., Tutin, C.E.G., White, L.J.T. & Wilkie, D.S. (2003) Catastrophic ape decline in western equatorial Africa. *Nature* **422,** 611–617.

Wanyama, F. (2005) *Ground Census of Mammals in Kibale National Park Uganda*. Unpublished Report of the Research and Monitoring Unit of the Uganda Wildlife Authority, Kampala, Uganda.

Wing, L.D. & Buss, I.O. (1970) Elephants and forests. *Wildlife Monogr.* **19,** 3–92.

(*Manuscript accepted 9 November 2009*)

doi: 10.1111/j.1365-2028.2009.01197.x