

How do human activities influence the status and distribution of terrestrial mammals in forest reserves?

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Tropical forests support a rich biodiversity of terrestrial mammals, yet our knowledge of the conservation of forest reserves is lacking. We investigate the relationship between human activities and the abundance of medium-sized terrestrial mammals within 4 forest reserves in Uganda. These reserves allow firewood collection, timber cutting, gardening, and pole cutting. Illegal hunting also takes place. We found a general decline in terrestrial mammal signs in the reserves compared to the better protected adjacent Kibale National Park. Signs of aardvarks, bushbucks, bush pigs, duikers (blue and red), giant pangolin, giant forest hogs, porcupines, and jackals are still present in some of our reserves.

Key words: bushbuck, bush pig, duiker, forest reserves, giant forest hog, pangolin, terrestrial mammals

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Tropical forests are well-known for their high diversity of terrestrial mammals (Ceballos and Ehrlich 2002), in fact they support far more than 50% of all known species of large- and medium-sized ungulates (National Research Council 1992), and many such terrestrial mammals are incapable of surviving in modified habitats or open grasslands (Struhsaker 1997; Wanyama et al. 2009), particularly if hunted (Peres 2000; Blake and Hedges 2004; Reyna-Hurtado et al. 2010).

Tropical forests are being degraded and destroyed at a very high rate. Between 2000 and 2012, tropical forest loss increased by 2,101 km² per year (Hansen et al. 2013). This high rate of deforestation is largely driven by increased human population size and consumption rates (Isabirye-Basuta and Lwanga 2008; Chapman et al. 2010). In Africa, local communities living adjacent to many forests typically practice subsistence shifting agriculture but are highly dependent on forest products (Naughton-Treves et al. 2011). These forest products include fuelwood, bushmeat, medicinal plants, timber, and building poles. This extraction creates forest gaps and often disrupts ecosystem function (Beckman and Muller-Landau 2007; Wright et al. 2007). This process has been going on for centuries (Hamilton et al. 1986) but has recently increased dramatically in intensity and led to a reduction or total disappearance of some ungulate populations in unprotected forests through local, national, and international processed (Wanyama et al. 2009; Chapman et al. 2013). Even many protected areas have failed to adequately protect some terrestrial mammal species (Redford and Richter 1999; Bruner et al. 2001; Seiferling et al. 2012; Maisels et al. 2013). In Uganda, the country of this study, the situation is critical. Closed-canopy tropical forest once covered 20% of the country's land area, but deforestation has reduced this to just 3% (Howard et al. 2000). Furthermore, between 1990 and 2000, Uganda lost 18% of its remaining forest (Howard et al. 2000) and the most recent estimate suggests that the annual rate of loss of tropical forest is 7% (Pomeroy and Tushabe 2004). Because most of Uganda's national parks were established in grasslands (MISR Makerere University Institute for Social Research 1989), national parks offer little protection for forest mammals that rely forested ecosystems. Unfortunately, forest reserves are vulnerable to anthropogenic pressures (Bruner et al. 2001). Protected areas are generally effective at preventing land clearing but are less effective at preventing logging, human-created fire, cattle grazing, and bushmeat hunting (Bruner et al. 2001; Naughton-Treves et al. 2011), which typically are initiated by members of nearby communities (West et al. 2006; Hartter et al. 2011). However, within protected areas, national parks are viewed as more effective at protecting wildlife than forest reserves (Plumptre and Reynolds 1994; Fashing and Cords 2000; Plumptre et al. 2001; S. Mugume, pers. obs.).

Despite their general ineffectiveness, forest reserves form a large percentage of the protected tropical forests in many regions, are typically considered in estimates of remaining forest and mammal habitat (Baranga 2004; Chapman et al. 2006; FAO 2010, 2012), and are often assumed to be an effective means of protecting terrestrial mammals (Plumptre et al. 2003). However, the ability of forest reserves to conserve mediumsized mammals is poorly quantified, particularly in the light of bushmeat hunting. Subsistence and commercial hunting are having devastating impacts on terrestrial mammal populations in many regions (Redford 1992; Wilkie et al. 1992; Bowen-Jones and Pendry 1999). From case studies, it is clear that bushmeat hunting provides a major source of food for many local communities, and primates and ungulates are often the target of such hunting activities (Martin 1983; Peres 1996; Fa et al. 2002). Compared to many other taxa, most terrestrial mammals are relatively large bodied, giving a good return of meat for hunting investment, and are considered highly palatable.

Here, we investigate the relationship between human activities and the relative abundance of medium-sized terrestrial mammals within 4 forest reserves in Uganda. These reserves allow firewood collection, timber cutting, gardening, and pole cutting, and illegal hunting also occurs.

MATERIALS AND METHODS

Study area.—The study was conducted in 4 forest reserves (Matiiri, Itwara, Kibego, and Buhungiro; Fig. 1) from September 2008 to April 2010. The reserves all lie in Western Uganda. These forests are remnants of extensive tropical forest that once stretched from the west coast of Africa to the east beyond the Kenyan border; however, because of increased human settlement and agricultural development, these forests have been isolated (Hamilton 1974, 1984; Hamilton et al. 1986). These

reserves are close to Kibale National Park (795 km²) and Semuliki Wildlife Reserve (220 km²), which are important mammal habitats and have a higher protection status than the 4 forests (Chapman and Lambert 2000; Mugume 2003).

Itwara and Kibego are surrounded by a high human population density of 172–199 people/km², respectively, while Matiiri and Buhungiro are surrounded by a lower human population density of 95–117 people/km² (Government of Uganda 2002). The human activities practiced around the 4 forests also differ; Kibego and Itwara are surrounded by large tea plantations, while Matiiri and Buhungiro are surrounded by subsistence farming (Government of Uganda 1996, 2000, 2002). Matiiri (64 km²) and Itwara (84 km²) are relatively bigger than Kibego (12 km²) and Buhungiro (8 km²). All the 4 forests are managed by Uganda National Forest Authority which allows some human activities alongside conservation. The tradition of the cultures in the area is that men enter the forest, as women are scared of what could happen if they were alone in the forest: women only collect fuel wood on forest edges (Naughton-Treves et al. 2006).

Transects and footprints/signs (tracking stations).—Mediumsized mammals were counted along transects using standard line transect census methodology. Depending on its size, the number and length of transects in each forest reserve varied, with a minimum length of 2 km and a maximum length of 8 km. Transects were visited between 0800 and 1200 h and 1500 and 1900 h once a month for the first 8 months and then twice a month for the next 12 months (repeat censuses on the same day were averaged). We identified and recorded all mammal sign, such as pellets and footprints, that was visible from the transect.

To obtain another estimate of relative abundance of largeand medium-sized mammals, following the method described in the literature (Zanne and Chapman 2001; Zanne et al. 2001; Conover and Linde 2009). We established 1×1-m tracking

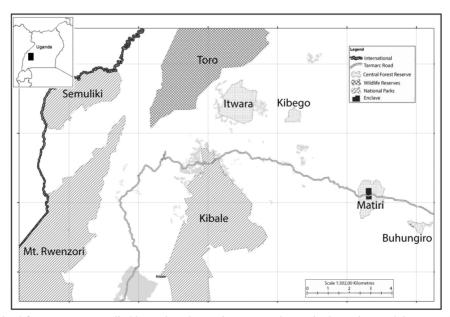


Fig. 1.—The location of the 4 forest reserves studied here, the other major protected areas in the region, and the general area within Uganda. The black square on the map of all Uganda is the study area where the forest reserves were located.

stations 500 m apart along each transect. The day before sampling, each plot was cleared of vegetation and dug to loosen the earth, so that any animal that stepped in the plot would leave a clear print. In cases where the footprints could not be identified, photographs were taken and later interpreted using the mammal guide book (Stuart and Stuart 2009). After each observation, plots were cleaned by releveling the loosened soil so that new footprints could be captured for identification and counting during the next visit. These plots were monitored once every 2 weeks during the last 12 months.

Any human signs along the transects was mapped using a GPS and overlaid on a map of the distribution of each terrestrial mammal. It is very rare to find people engaged in illegal activities; for this reason, to establish the intensity of such activities, indirect signs were used of human disturbance (Olupot and Chapman 2006). Signs of pitsawying, charcoal processing, pole cutting, hunting, grazing, gardening, and fuel-wood collection were recorded along transects used for censusing mammals. Further data on illegal activities were collected in 25×25-m plots that were set every 500 m along the transect. Each plot was established 50 m from the center of the transect. The cumulative number of signs of illegal human activities along the transects and in these plots were calculated to give a relative index of intensity of signs per km² and these values were compared among reserves. To establish if animals favored closed forest to open forest, average canopy cover for each transect was estimated using a densitometer every 100 m.

Relative abundance of mammals was calculated based only on footprints which were more abundantly and more consistently seen than any other sign. Data from the transect and tracking stations were summed to represent the relative abundance of animals and similarly data from the transects and the 25×25-m plots were summed to obtain a relative index of human disturbance. We used the Kruskal-Wallis test to examine if the relative abundance of mammals differed among forest reserves. Kendall's correlations were performed to test the relationship between the index of human activity, average percent canopy cover, and mammal relative abundance. Transects were considered independent in the statistical analysis; thus, the samples size is 20. It is reasonable to use transects as independent units as resources and habitat quality changes rapidly, and it is not necessary to us a Bonferroni correction factor when examining multiple variables (e.g., human activity, canopy cover—Perneger 1998; Nakagawa 2004).

The research followed the guidelines of American Society of Mammalogists and was approved by National Council for Science and Technology of Uganda, the Uganda Wildlife Authority, the National Forest Authority, and McGill University Animal Care.

RESULTS

Indirect signs (dung, footprints, diggings, feeding sites, and burrow pits) of 9 species of medium-sized terrestrial mammals were seen across all 4 of the forest reserves combined. Footprints were the most common sign both along the transect

and within tracking stations. Out of these 9 species, Itwara had the richest community with 8, Matiiri had 7, while Kibego and Buhungiro each had 5 species. Bush pigs (Potamochoerus larvatus), porcupines (Erethizon dorsatum), and 2 duiker species (red Cephalophus natalensis and blue Philantomba monticola duiker species were combined as their prints are difficult to distinguish; however, there were instances where tracks could be differentiated) were found in all forest reserves. Giant forest hogs (Hylochoerus meinertzhageni) were only found in Itwara (Table 1). A few direct sightings of blue or red duiker, bush pigs, and baboons (Papio anubis) were recorded in Itwara, Matiiri, and Buhungiro (Table 1). Burrow pits of aardvarks (Orycteropus afer) were only observed in Itwara and Matiiri and bushbucks (Tragelaphus scriptus) were only present in Itwara and Kibego. Nests of giant pangolins (Manis gigantea) were seen in Itwara and Kibego, but no other signs of this species were observed (Table 1). In Matiiri, Buhungiro, and Itwara, signs of medium-sized mammals were found along all transects, while at Kibego, signs were only found on the 2 lines that were close to the edge.

Based only on footprints, Matiiri had the highest relative abundance of bush pigs, followed by Itwara, Kibego, and lastly Buhungiro (Table 2). Bushbuck footprints were only seen in Kibego and Itwara, where one bushbuck was seen and dung was recorded. Footprints of giant pangolin were only seen in Matiiri (Table 2). Footprints of porcupines were only seen in Matiiri and Buhungiro, but in Itwara and Kibego, burrow pits of porcupines were recorded. Jackals were recorded in Matiiri and Buhungiro (Table 1). Encounter rates of signs of bush pigs and duiker in the 4 forests were not significantly different (n = 20, P = 0.26 for both species). Other species were not evaluated given the sample size per reserve.

When we examined if the relative abundance of different species was associated with canopy cover, we discovered that only porcupines were negatively correlated with canopy cover (Table 3).

Human activities were grouped into 3 categories: 1) those thought to be related to hunting which included snares and dog footprints; 2) those known to cause changes in ground vegetation through agriculture which included grazing and gardening; and 3) those that change canopy cover (wood harvest, charcoal processing, pitsawying, and pole cutting). Charcoal processing was only seen in Itwara and Matiiri. Gardens were only seen in Matiiri and Buhungiro, while signs of hunting were seen in all forests (Table 4). There was no significant difference between the encounter rates of pole cutting, foot paths, hunting, grazing, pitsawying, charcoal processing, and other human activities among the 4 reserves (n = 20, P = 0.26 in all cases).

In Itwara, there was a positive correlation between incidences of baboons and number of hunting signs (Kendall; P = 0.006, n = 17); a negative correlation between number of duikers and number of pitsawying sites (P = 0.044, n = 17), and a negative correlation between number of pitsawying sites and number of blue duikers (P = 0.044, n = 17), when blue duiker prints could be distinguished from those of red duiker.

Table 1.—Animal sign encounter rate per km of transect in forest reserves in Uganda (T is the transect number). The porcupine, pangolin, and baboon are semi-arboreal, so the estimates of encounter rate will be an underestimate, but should be comparable among reserves.

Forest	Animal species	Type of observation	Encounter rate (individuals/km)						
			T 1	T 2	Т3	T 4	T 5	T 6	Total
Buhungiro	Aardvark	Sign	0.03	0.03	0.02				0.03
Buhungiro	Duiker	Animals seen	0.03	0.00	0.05				0.03
Buhungiro	Porcupine	Sign	0.27	0.12	0.23				0.21
Buhungiro	Bush pig	Sign	0.52	0.15	0.64				0.45
Buhungiro	Duiker	Sign	0.03	0.00	0.00				0.01
Itwara	Aardvark	Sign	0.00	0.00	0.00	0.00	0.00	0.01	0.00
Itwara	Duiker	Animals/signs seen	0.08	0.08	0.06	0.08	0.09	0.04	0.07
Itwara	Bushbucks	Animals/signs seen	0.00	0.00	0.00	0.00	0.01	0.00	0.00
Itwara	Giant pangolin	Animal seen	0.00	0.00	0.00	0.01	0.00	0.00	0.00
Itwara	Porcupine	Animal seen	0.00	0.01	0.01	0.00	0.00	0.01	0.00
Itwara	Bush pigs	Animal seen	0.12	0.12	0.15	0.18	0.17	0.11	0.14
Itwara	Giant forest hogs	Sign	0.00	0.00	0.00	0.01	0.00	0.00	0.00
Itwara	Baboons	Animals and signs seen	0.02	0.04	0.04	0.00	0.05	0.02	0.03
Kibego	Giant pangolin	Sign	0.00	0.00	0.01				0.01
Kibego	Porcupine	Sign	0.06	0.00	0.05				0.05
Kibego	Bush pigs	Sign	0.16	0.03	0.06				0.10
Kibego	Bushbuck	Sign	0.00	0.00	0.01				0.01
Matiiri	Aardvark	Sign	0.02	0.03	0.00	0.01	0.00	0.00	0.01
Matiiri	Duiker	Animal seen	0.01	0.01	0.00	0.02	0.02	0.00	0.00
Matiiri	Giant pangolin	Animal seen	0.01	0.03	0.00	0.00	0.00	0.00	0.01
Matiiri	Porcupine	Animal seen	0.05	0.09	0.04	0.15	0.15	0.05	0.09
Matiiri	Jackal	Animals/signs seen	0.01	0.02	0.00	0.01	0.01	0.00	0.01
Matiiri	Bush pig	Sign	0.10	0.24	0.21	0.36	0.39	0.14	0.22
Matiiri	Baboons	Animal seen	0.01	0.01	0.03	0.03	0.02	0.04	0.02

Table 2.—Encounter rates (number/km transect) of footprints per animal species in different forest reserves in Uganda.

Animal species	Kibego	Buhungiro	Itwara	Matiiri
Bushbuck	0.013	0.000	0.000	0.000
Bush pig	0.594	3.034	0.722	1.144
Duiker	0.000	0.229	0.427	0.084
Giant pangolin	0.000	0.000	0.000	0.012
Giant forest hog	0.000	0.000	0.023	0.000
Porcupine	0.000	0.009	0.000	0.029
Jackal	0.000	0.038	0.000	0.002

Table 3.—Relationship between animal species encounter rates in forest reserves in Uganda and percent canopy cover.

Species	Kendall's correlation coefficient	P (2-tailed)	
Aardvark	-0.331	0.088	
Duiker	0.035	0.847	
Porcupine	-0.402	0.026	
Bush pig	-0.233	0.183	
Bushbuck	0.232	0.260	
Pangolin	0.064	0.751	
Forest hog	0.258	0.209	
Baboon	-0.125	0.502	

There was a negative correlation between the distance from the edge of the forest at Itwara and canopy cover and the number of footprints of bush pigs (P = 0.014, n = 1,328 and P = 0.005, n = 1,328, respectively). There was a positive correlation between number of footprints of bushbucks, red duikers, and the number of footprints of human at Itwara (P < 0.001, n = 1,328 and P < 0.001, n = 1,328, respectively) and a positive correlation between number of footprints of humans and number of footprints of civets, jackals, and genets (P = 0.005,

Table 4.—Encounter rate of signs (number/km transect) indicating presence of human activities in forest reserves in Uganda.

	Buhungiro	Itwara	Kibego	Matiiri
Charcoal processing	0.000	0.013	0.006	0.025
Gardening	0.096	0.000	0.000	0.014
Grazing	0.297	0.001	0.056	0.273
Hunting	0.010	0.038	0.050	0.025
Other human activities	0.211	0.083	0.285	0.115
Pitsawying	0.019	0.008	0.025	0.031
Pole cutting	0.038	0.013	0.235	0.041
Total signs	0.670	0.156	0.656	0.513

n = 1,328; P = 0.001, n = 1,328; and P = 0.012, n = 1,328, respectively).

In Matiiri, there was a positive correlation between signs of bush pigs, number of grazing sites, and signs of hunting (P = 0.035, n = 18 and P = 0.001, n = 18, respectively); a positive correlation between signs of duikers and number of charcoal processing sites seen (P = 0.038, n = 18); a positive correlation between number of baboons and number of hunting signs (P = 0.04, n = 18); and a positive correlation between

number of baboons and number of pitsawying sites (P = 0.032, n = 18). We combined other low-impact human activities such as firewood collection, human footprints, collection of medicinal plants, and accessing water sources into one category called "other human activities" and only baboons were positively correlated to these signs of human activities (P = 0.002, P = 18).

The number of footprints of duiker, dog(P < 0.001, n = 1,537), cattle (P < 0.001, n = 1,537), and goats were also positively related (P < 0.001, n = 1,537). In Buhungiro, human footprints are spread throughout the forest but had a positive correlation with the occurrence of baboon prints (P < 0.001, n = 352). In Kibego, there was a positive correlation between number of footprints of goats and number of footprints of baboons, duikers, genets, giant forest hogs, and civets (P = 0.016, n = 638; P = 0.03, n = 638; P = 0.026, n = 638; P = 0.01, n = 638; P < 0.001, n = 638; and P < 0.001, n = 638, respectively).

The number of dog prints was related to the number of prints of bush pigs, baboons, duikers, and genets (P < 0.001, n = 638; P = 0.04, n = 638; P = 0.05, P = 0.05, P = 0.05, P = 0.011, P = 0.011

DISCUSSION

Several medium-sized mammals were generally positively correlated with human presence in all forest reserves and only duikers in Itwara were negatively associated with pitswaying. This pattern likely reflects the skills of the hunters to go to the areas where game is most abundant. Some species showed no pattern with human presence, likely because they were detected only a few times (e.g., giant forest hog, giant pangolin, and bushbuck). The low relative abundance of these species suggests that they are not doing well in these small, highly perturbed forest reserves as compared to large protected areas. For example, giant forest hog and bush buck are common inhabitant of Kibale National Park and the latter can even be seen in the biological station on a daily basis (R. Reyna-Hurtado and C. A. Chapman, pers. obs.). These patterns are very similar to other geographic areas. For example, white-lipped peccary (Tayassu pecari) and tapir (Tapirus bairdii) are the first species to disappear when humans colonize new forests in the Americas (Leopold 1959; Reyna-Hurtado and Tanner 2007; Reyna-Hurtado et al. 2010).

Bush pigs were positively correlated with grazing and hunting signs, which likely indicates that hunters look for signs of bush pigs and thereby setting their snares and traps where the probability of capture is the highest. However, the high persistence of this species in the 4 sites despite being a favorite prey for hunters indicates that this species is resistant to human impact and has strategies to survive in perturbed areas. This phenomenon is similar to the collared peccary (*Pecari tajacu*), which despite being the most hunted animal in many forests of Mexico are still present in similar numbers in reserves as in protected areas (Reyna-Hurtado and Tanner 2007).

Duikers were positively associated with grazing, charcoal processing, hunting, and pitswaying in Matiiri and also positively associated with hunting in Kibego. However, duiker numbers were negatively associated to pitsawying in Itwara. Browsing duikers tend to move to open spaces to look for grass and sunlight and thus they are likely attracted to the same areas as domestic animals. In Matiiri, where most pitsawying sites were old, duikers were positively associated with pitsawying. However, in Itwara, most sites were new and duikers were negatively associated with pitsawying, which likely reflects the state of regeneration. Similarly, in Neotropical forest, deer species (white-tailed deer Odocoileus virginianus and brocket deer Mazama temama and M. pandora) show a pattern of living in closed-canopy forest but take advantage of openings to browse (Reyna-Hurtado and Tanner 2005; Weber 2005; Bello-Gutiérrez et al. 2010). Drawing inferences to all forest reserves must be made with caution, as logistical constraints limited us to sampling only 4 forest reserves. Sampling more reserves is required to test the generality of our findings.

Providing increased protection for these mammal populations will be difficult and will take a large multifaceted approach. One of those approaches could be to establish research stations or ecotourism sites, which have been shown to reduce poaching (Struhsaker et al. 2005). This phenomenon is poignantly illustrated by a study in Tai National Park, Cote d'Ivoire. A park-wide survey of the density of monkeys in Tai illustrated that regardless of primate species, density was 100 times higher near the protected research station and tourism site than the remainder of the park (N'Goran et al. 2012). Similarly, in Moukalaba Doudou National Park, Gabon surveys demonstrated that ape nest density was 3 times lower at the park borders near human population centers, as compared to the park interior (Kuehl et al. 2009).

Another component for the protection of these forest reserves should involve new methods of conservation education. Public outreach is a conservation strategy that has been employed for decades. The idea being that if conservation biologists can illustrate to the community the value of a protected area, they will not exploit its resources. Unfortunately, contrary to expectations, studies in Africa have demonstrated that outreach programs designed to promote positive attitudes are seldom associated with successful conservation outcomes (Struhsaker et al. 2005). It is our opinion that these negative results do not mean that this approach should be abandoned, but rather we should learn from past experiences and make the approach more effective. In fact, there is a resurgence of the application of this approach (Padua 2010; Savage et al. 2010) and its careful longterm evaluation (Jacobson 2010; Kuhar et al. 2010) and some of the original problems of such programs (Struhsaker et al. 2005; Kasenene and Ross 2008) are being addressed. Also new outreach approaches should be investigated. We have initiated one such new approach involving the union of the provision of health care and conservation; namely, the delivery of subsided health care to local communities bordering Ugandan national parks through the Mobile Health Clinic System (Uganda Wildlife Authority) and the establishment of a building that is

a large clinic (Chapman et al. 2015). The mobile health clinic is a means to reach many people, in fact it is estimated that approximately 30,000 people a year will be receive treatment and the outreach associated with the clinics will reach many more people.

In conclusion, we suggest that forest reserve size is a major factor in wildlife conservation, as has been suggested in parks (Simberloff 1998). We also show that presence of human activities threatens the existence of terrestrial mammals in any protected areas and thus strongly recommends reduction in the presence and number of humans in forests reserves, including enforcement of laws, education programs, and, potentially, the establishment of research centers or ecotourism sites.

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LITERATURE CITED

- BARANGA, D. 2004. Forest fragmentation and primate survival status in non-reserve forests of the Kampala area, Uganda. African Journal of Ecology 42:70–77.
- BECKMAN, N. G., AND H. C. MULLER-LANDAU. 2007. Differential effects of hunting on pre-dispersal seed predation and primary and secondary seed removal of 2 neotropical tree species. Biotropica 39:328–339.
- Bello- Gutiérrez, J., R. Reyna-Hurtado, and W. Jorge. 2010. Central American red brocket deer *Mazama temama* (Kerr 1792). Pp. 166–172 in Neotropical cervidology: biology and medicine of Latin American deer (J. M. Barbanti-Duarte and S. Gonzalez, eds.). International Union for the Conservation of Nature, Gland, Switzerland.
- BLAKE, S., AND S. HEDGES. 2004. Sinking the flagship: the case of forest elephants in Asia and Africa. Conservation Biology 18:1191–1202.
- Bowen-Jones, E., and S. Pendry. 1999. The threat to primates and other mammals from the bushmeat trade in Africa, and how this threat could be diminished. Oryx 33:233–246.
- Bruner, A. G., R. E. Gullison, R. E. Rice, and G. A. B. da Fonseca. 2001. Effectiveness of parks in protecting tropical biodiversity. Science 291:125–128.
- CEBALLOS, G., AND P. R. EHRLICH. 2002. Mammal population losses and the extinction crisis. Science 296:904–907.
- CHAPMAN, C. A., ET AL. 2013. Going, going, gone: a 15-year history of the decline of primates in forest fragments near Kibale National Park, Uganda. Pp. 89–104 in Primates in fragments: complexity and resilience (L. K. Marsh and C. A. Chapman, eds.). Springer, New York.
- CHAPMAN, C. A., AND J. E. LAMBERT. 2000. Habitat alteration and the conservation of African primates: case study of Kibale National Park, Uganda. American Journal of Primatology 50:169–185.

- Chapman, C. A., M. J. Lawes, and H. A. C. Eeley. 2006. What hope for African primate diversity? African Journal of Ecology 44:1–18
- CHAPMAN, C.A., T. T. STRUHSAKER, J. P. SKORUPA, T. V. SNAITH, AND J. M. ROTHMAN. 2010. Understanding long-term primate community dynamics: implications of forest change. Ecological Applications 20:179–191.
- CHAPMAN, C. A., ET AL. 2015. Providing health care to promote people-park relations. Oryx. doi: 10.1017/S0030605313001592.
- CONOVER, R. R., AND E. T. LINDE. 2009. Mud track plots: an economical, noninvasive mammal survey technique. Southeastern Naturalist 8:437–444.
- FA, J. E., C. A. PERES, AND J. MEEUWIG. 2002. Bushmeat exploitation in tropical forests: an intercontinental comparison. Conservation Biology 16:232–237.
- FAO. 2010. The global forest resource assessment 2010. Food and Agriculture Organization of the United Nations, Rome, Italy.
- FAO. 2012. Forest products statistics. http://www.fao.org/forestry/statistics/en/. Accessed 20 July 2014.
- Fashing, J. P., and M. Cords. 2000. Diurnal primate densities and biomass in the Kakamega Forest: an evaluation of census methods and a comparison with other forests. American Journal of Primatology 50:139–152.
- GOVERNMENT OF UGANDA. 1996. Forest management plan. Forest Department, Kampala, Uganda.
- GOVERNMENT OF UGANDA. 2000. Uganda participatory poverty assessment process: Kabarole District report, Ministry of Finance, Planning and Economic Development. Government of Uganda, Kampala, Uganda.
- GOVERNMENT OF UGANDA. 2002. National housing and rural settlement census. Census Bureau, Kampala, Uganda.
- Hamilton, A. C. 1974. Distribution patterns of forest trees in Uganda and their historical significance. Vegatatio 29:21–35.
- Hamilton, A. C. 1984. Deforestation in Uganda. Oxford University Press, Oxford, United Kingdom.
- HAMILTON, A. C., D. TAYLOR, AND J. C. VOGEL. 1986. Early forest clearance and environmental degradation in south-west Uganda. Nature 320:164–167.
- Hansen, M. C., et al. 2013. High-resolution global maps of 21st-Century forest cover change. Science 342:850–853.
- HARTTER, J., A. GOLDMAN, AND J. SOUTHWORTH. 2011. Responses by households to resource scarcity and human-wildlife conflict: issues of fortress conservation and the surrounding agricultural landscape. Journal of Nature Conservation 19:79–86.
- Howard, P. C., ET AL. 2000. Protected area planning in the tropics: Uganda's national system of forest nature reserves. Conservation Biology 14:858–875.
- ISABIRYE-BASUTA, G. M., AND J. S. LWANGA. 2008. Primate populations and their interactions with changing habitats. International Journal of Primatology 29:35–48.
- JACOBSON, S. K. 2010. Effective primate conservation education: gaps and opportunities. American Journal of Primatology 72:414–419.
- KASENENE, J. M., AND E. A. Ross. 2008. Community benefits from long-term research programs: a case study from Kibale National Park, Uganda. Pp. 99–114 in Science and conservation in African forests: the benefits of long-term research (R. W. Wrangham and E. A. Ross, eds.). Cambridge University Press, Cambridge, United Kingdom.
- Kuehl, H. S., C. Nzeingui, S. L. D. Yenom, B. Huijbregts, C. Boesch, and P. D. Walsh. 2009. Discriminating between

- village and commercial hunting of apes. Biological Conservation 142:1500–1506.
- Kuhar, C. W., T. L. Bettinger, K. Lehnhardt, O. Tracy, and D. Cox. 2010. Evaluating for long-term impact of an environmental education program at the Kalinzu Forest Reserve, Uganda. American Journal of Primatology 72:407–413.
- LEOPOLD, A. S. 1959. Fauna silvestre de México. Instituto Mexicano de Recursos Naturales Renovables, Mexico City, Mexico.
- MAISELS, F., ET AL. 2013. Devastating decline of forest elephants in Central Africa. PLoS One 8:e59469.
- MARTIN, G. 1983. Bushmeat in Nigeria as a natural resource with environmental implications. Environmental Conservation 10:125–132.
- MISR MAKERERE UNIVERSITY INSTITUTE FOR SOCIAL RESEARCH. 1989. Settlement in Forest Reserves, Game Reserves, and National Parks. Makerere University, Kampala, Uganda.
- MUGUME, S. 2003. Evaluation of chimpanzee censusing methods and an estimation of the snare density in Kibale National Park. M.S. thesis, Makerere University, Kampala, Uganda.
- NAKAGAWA, K. 2004. A farewell to Bonerroni: the problems of low statistical power and publication bias. Behavioural Ecology 12:1044–1045.
- NATIONAL RESEARCH COUNCIL. 1992. Conserving biodiversity: a research agenda for development agencies. National Academies Press, Washington, D.C.
- NAUGHTON-TREVES, L., J. ALIX-GARCIA, AND C. A. CHAPMAN. 2011. A decade of forest lossand economic growth around Kibale National Park, Uganda: lessons of poverty reduction and biodiversity conservation. Proceedings of the National Academy of Sciences 108:13919–13924.
- Naughton-Treves, L., D. M. Kammen, and C. A. Chapman. 2006. Burning biodiversity: woody biomass use by commercial and subsistence groups in western Uganda. Biodiversity Conservation 34:232–241.
- N'GORAN, P. K., ET AL. 2012. Hunting, law enforcement, and African primate conservation. Conservation Biology 26:567–571.
- OLUPOT, W., AND C. A. CHAPMAN. 2006. Human encroachment and vegetation change in isolated forest reserves: the case study of Bwindi impenetrable National Park, Uganda. Pp. 127–142 in Emerging threats to tropical forests (W. F. Laurance and C. A. Peres, eds.). University of Chicago Press, Chicago, Illinois.
- Padua, S. M. 2010. Primate conservation: integrating communities through environmental education programs. American Journal of Primatology 72:450–453.
- Perneger, T. V. 1998. What's wrong the Bonferroni adjustments. British Medical Journal 316:1236–1238.
- Peres, C. A. 1996. Population status of white-lipped *Tayassu pecari* and collared peccaries *T. tajacu* in hunted and unhunted Amazonian forest. Biological Conservation 77:115–123.
- Peres, C. A. 2000. Evaluating the impact and sustainability of subsistence hunting at multiple Amazonian forest sites. Pp. 31–57 in Hunting for sustainability in tropical forests (J. F. Robinson and E. L. Bennett, eds.). Columbia University Press, New York.
- PLUMPTRE, A. J., ET AL. 2003. The biodiversity of the Albertine Rift. Wildlife Conservation Society, Kampala, Uganda.
- Plumptre, A. J., S. Mugume, D. Cox, and C. Montgomery. 2001. Chimpanzee and large mammal surveys of Budongo Forest Reserve and Kibale National Park. Report to Wildlife Conservation Society on surveys in Western Uganda, Wildlife Conservation Society, Kampala, Uganda.
- PLUMPTRE, A. J., AND V. REYNOLDS. 1994. The effect of selective logging on the primate populations in the Budongo Forest Reserve, Uganda. Journal of Applied Ecology 31:631–641.

- POMEROY, D., AND H. TUSHABE. 2004. The state of Uganda's biodiversity 2004. Makerere University, Kampala, Uganda.
- REDFORD, K. 1992. The empty forest. Bioscience 41:412–422.
- REDFORD, K. H., AND B. D. RICHTER. 1999. Conservation of biodiversity in a world of use. Conservation Biology 13:1246–1256.
- REYNA-HURTADO, R., E. NARANJO, C. A. CHAPMAN, AND G. W. TANNER. 2010. Hunting patterns, population density, group size, and conservation of the white-lipped peccary (*Tayassu pecari*) in the Calakmul region of Mexico. Oryx 44:88–96.
- REYNA-HURTADO, R., AND G. W. TANNER. 2005. Habitat preferences of an ungulate community in Calakmul Forest, Campeche, Mexico. Biotropica 37:676–685.
- REYNA-HURTADO, R., AND G. W. TANNER. 2007. Ungulate relative abundance in hunted and non-hunted sites in Calakmul Forest (Southern Mexico). Biodiversity Conservation 16:743–756.
- SAVAGE, A., R. GUILLEN, I. LAMILLA, AND SOTO, L. 2010. Developing an effective community conservation program for cotton-top tamarins (*Saguinus oedipus*) in Colombia. American Journal of Primatology 72:379–390.
- SEIFERLING, I. S., R. PROULX, P. R. PERES-NETO, L. FAHRIG, AND C. MESSIER. 2012. Measuring protected-area isolation and correlations of isolation with land-use intensity and protection status. Conservation Biology 26:610–618.
- SIMBERLOFF, D. 1998. Flagships, umbrellas, and keystones: is single-species management passe in the landscape era? Biological Conservation 83:247–257.
- 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., P. J. STRUHSAKER, AND K. S. SIEX. 2005. Conserving Africa's rain forests: problems in protected areas and possible solutions. Biological Conservation 123:45–54.
- STUART, C., AND M. STUART. 2009. Mammals of East Africa. Random House StruikNature, London, United Kingdom.
- Wanyama, F., R. Muhabwe, A. J. Plumptre, C. A. Chapman, and J. M. Rothman. 2009. Censusing large mammals in Kibale National Park: evaluation of the intensity of sampling required to determine change. African Journal of Ecology 48:953–961.
- Weber, M. 2005. Ecology and conservation of sympatric tropical deer populations in the Greater Calakmul Region, south-eastern Mexico. University of Durham, Durham, United Kingdom.
- West, P., J. Igoe, and D. Brockington. 2006. Parks and peoples: the social impact of protected areas. Annual Review of Anthropology 35:251–277.
- WILKIE, D. S., J. G. SIDLE, AND G. C. BOUNDZANGA. 1992. Mechanized logging, market hunting and a bank loan in Congo. Conservation Biology 6:570–580.
- WRIGHT, S. J., ET AL. 2007. The plight of large animals in tropical forest and the consequences for plant regeneration. Biotropica 39:289–291.
- Zanne, A. E., and C. A. Chapman. 2001. Expediting reforestation in tropical grasslands: distance and isolation from seed sources in plantations. Ecological Applications 11:1610–1621.
- ZANNE, A. E., B. KEITH, C. A. CHAPMAN, AND L. J. CHAPMAN. 2001. Protecting terrestrial mammal communities: potential role of pine plantations. African Journal of Ecolgy 39:399–401.
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