

Contents lists available at [ScienceDirect](http://www.sciencedirect.com)

Biological Conservation

journal homepage: www.elsevier.com/locate/biocon

Camera-trapping forest–woodland wildlife of western Uganda reveals how gregariousness biases estimates of relative abundance and distribution

Adrian Treves^{a,*}, Polycarp Mwima^b, Andrew J. Plumptre^b, Sam Isoke^b

^a Nelson Institute for Environmental Studies, University of Wisconsin–Madison, 30A Science Hall, 550 North Park St., Madison, WI 53706, USA

^b Wildlife Conservation Society, P.O. Box 7487, Kampala, Uganda

ARTICLE INFO

Article history:

Received 28 September 2009

Received in revised form 23 November 2009

Accepted 24 November 2009

Keywords:

Biodiversity

Duiker

Giant forest hog

Group living

Leopard

Mark-recapture

Non-invasive monitoring

ABSTRACT

Camera traps are increasingly used to estimate relative abundance and distribution of wildlife. These methods are powerful and efficient ways to inventory multiple species simultaneously and count rare, secretive individuals across landscapes. However the estimation methods demand assumptions about relative capture probability that may not hold well for gregarious animals. We present results from the first systematic, camera-trap study in forest–woodland, western Uganda. Within a landscape of seven protected areas with globally important biodiversity, we detected >36 species of large mammals and birds in 8841 camera-trap days. Species photographed in groups of two or more individuals produced higher estimates of relative abundance and wider distribution than species photographed as single individuals. We propose these findings reflect higher detectability for animals that forage or travel in groups. We discuss how capture–recapture theory should be adapted to account for both non-independence among individuals in groups and for the interaction between individual and temporal variation in capture probability. We also identify several species that deserve greater conservation attention in Uganda and beyond. Among them, leopards were unexpectedly rare, especially when compared to the sympatric African golden cat. We recommend against a recent policy on leopard trophy hunting, at least in western Uganda.

© 2009 Elsevier Ltd. All rights reserved.

1. Introduction

Monitoring multiple wildlife species across a wide area can be prohibitively costly in time, personnel, and resources (Field et al., 2005; Gompper et al., 2006; Long et al., 2007; Manley et al., 2004). Thus automatic cameras triggered by motion or body heat are increasingly being applied to species inventories, abundance estimation, and evaluation of conservation efforts (Balme et al., 2009; McCarthy et al., 2008). Such “camera traps” may also reveal humans or associated threats to habitats and wildlife (O'Brien et al., 2003; van Schaik and Griffiths, 1996). Therefore the data from camera traps can help conservation planners to assess progress toward conservation goals and to target and design interventions (O'Brien et al., 2010; Wegge et al., 2004).

Camera traps are especially useful if conditions preclude direct observation or efficient indirect surveys. Wild animals using rugged topography, dense vegetation, or nocturnal conditions and those wary of humans have all been successfully photographed using camera traps (Larrucea et al., 2007; Maffei et al., 2004; McCarthy et al., 2008; Silver et al., 2004). Camera traps provide pre-

cise estimates of the number of species of large (>1 kg), terrestrial mammals and birds (O'Brien et al., 2003; Tobler et al., 2008) and allow estimation of abundances based on individual identification for some species (Henschel and Ray, 2003; Karanth et al., 2004; Silver et al., 2004; Wegge et al., 2004). Abundance estimates from camera-trap surveys have also been validated by calibration with other methods with some caveats (Balme et al., 2009; O'Brien, 2008; O'Brien et al., 2003; Wegge et al., 2004). However, estimates of abundance and distribution from camera-trap studies must be treated with caution given the major potential bias arising from differential detectability of individuals or species.

Relative detectability is expected to correlate positively with time spent near camera sensors. The duration and also the frequency of visits may increase under several common conditions. If animals are large-bodied, slow-moving, or if wildlife is attracted to the cameras by novelty, lure or bait, then they may linger and produce numerous photos in one visit (Larrucea et al., 2007; Tobler et al., 2008; Zug, 2009). Commonly researchers avoid this by discarding photos of the same species within a set time interval such as 0.5 h (O'Brien et al., 2003). Similarly, the frequency of visits to camera-trap stations may increase if animals prefer microsites selected and accessible by researchers using camera traps (e.g., terrestrial vs. arboreal), if the animals have small home ranges, or if

* Corresponding author. Tel.: +1 608 890 1450; fax: +1 608 262 2273.

E-mail address: atreves@wisc.edu (A. Treves).

the wildlife habituate to signs of people (Larrucea et al., 2007; O'Brien et al., 2003). By the same logic, we predict that detectability may also increase with gregariousness and site fidelity as follows. Gregariousness may increase detectability in a number of ways. For a single source with descriptions of how diverse animals move in groups (see Boinski and Garber, 2000). Social facilitation occurs if one group-member draws the attention of others to an object; it has been demonstrated in studies of visual attention to associates and studies of foraging behavior in gregarious primates and birds (Treves, 2000; Vickery et al., 1991). Social facilitation could increase the number of different individuals photo-captured in the same group and thereby elevate the probability of recapturing a particular, marked individual. Furthermore, repeat visits over intervals of minutes to hours might occur if groups meander back and forth during foraging more than singletons. Gregarious animals that forage on small arthropods and concentrated fruits are noted for such meandering and return visits over various intervals (Robinson, 1986; Waser, 1981). Site fidelity such as territoriality or central place foraging (Larrucea et al., 2007; Waser and Wiley, 1979) would also tend to increase the frequency of revisits to a few camera stations. Differences between species in the duration of visits to foraging patches and the frequency of their revisits have been documented for many species (Boinski and Garber, 2000). In addition to increasing photo-captures at one or a few stations, gregariousness could increase the apparent spatial distribution of a species. Large groups tend to travel further than small groups with many species (Wrangham et al., 1993), hence larger groups may cross a greater number of different camera stations. Finally, species with nomadic movements or large numbers of dispersers might produce many scattered photos of the same individuals especially if cameras are distributed along habitual travel routes such as human-made paths (Maffei et al., 2004; Wegge et al., 2004). Social organization and individual differences in the costs and benefits of gregariousness underlie many of these predictions as short-term associations (e.g., mating associations), seasonal fluctuations in grouping, and behavior within groups produce differential patterns of association among individuals and among species. In short, complex, temporal and spatial variations in social behavior may affect the number of photos collected in a camera-trap survey and the temporal and spatial distribution of such photos.

Here we present results of the first camera-trap study of the forests and woodlands of western Uganda (Fig. 1). We present species inventories from 8841 camera trap-days at 192 separate stations in seven protected areas (Table 1). We present measures of species richness for a landscape pool of 36 taxa and estimates of spatial distribution at three scales. We explore relative detectability as a function of two estimates of gregariousness taken from our own study, as well as female body mass, female home range size, and microsite use, all estimated from the literature. We end by calling attention to several species needing conservation attention including information for an ongoing debate about hunting leopards (*Panthera pardus*) in Uganda.

2. Methods

We placed camera traps in seven protected areas (PAs, Fig. 1). Three were national parks (NPs) and four were Forest or Wildlife Reserves (Reserves) but average size of NPs and Reserves was the same (Table 1: median test $\chi^2 = 1.0$, $df = 1$, $P = 0.31$). The two categories experienced different levels of protection and management attention in Uganda (Howard, 1991; Uganda Wildlife Authority, 2000). All camera-trap (CT) stations were in the northern Albertine Rift, which stretches from the northern tip of Lake Albert to Lake Tanganyika, Tanzania. The Albertine Rift is one of the most species-rich regions on earth (Plumptre et al., 2007a). Four of the PAs in this landscape have been noted for species richness or high

numbers of endemic vertebrates and threatened species: Kibale NP, Bwindi NP, Rwenzori NP, and Kasyoha–Kitomi Reserve (Plumptre et al., 2007a). All the protected areas are ascribed to the Greater Virunga Landscape and adjoin densely settled areas or Virunga National Park, across the frontier of the Democratic Republic of Congo (Plumptre et al., 2007b; Treves et al., 2009).

We positioned CT stations (film Camtrakkers) in one of two ways. Where access was difficult (Kasyoha–Kitomi $n = 49$ CT stations, Maramagambo $n = 25$, and Kalinzu Reserves $n = 23$), we mapped transects by Systematic Segmented Trackline Sampling using DISTANCE software (Thomas et al., 2006). We then walked these transects, cut occasionally for access, and placed CT stations only where wildlife trails or sign crossed transects. In all other PAs, CT stations were placed along wildlife trails or within 6 m of a trail used by people or wildlife but no transects were cut because access was easier. No two CT stations were placed within 200 m of each other and most were 0.5–1 km apart, clustered in localities within PAs. The locations of individual CT stations are not necessarily discernible in our map due to scale but localities can be seen as clusters of CT station points (Table 1; Fig. 1). GPS locations of CT stations are available from the authors. Localities were distinguishable to the field teams by obvious habitat or topographical differences. Thus we adopted a stratified approach within each PA but the placement of CT stations was somewhat haphazard within the constraints of the criteria mentioned above. Indeed this study spanning a long period with two field team leaders (SI and PM) working at different PAs may include interobserver differences that add to or confound intersite and interannual variations. This raises the possibility that we under- or over-represented species that preferred the habitats accessible to us. This is a common bias in camera-trap studies – one alternative would have been to cut vegetation around camera traps to improve human access but that approach carries with it different biases.

We identified most wildlife photos to species (Appendix 1 for scientific names). However a few were difficult to distinguish or taxonomically unresolved so we pooled them at the level of genus or family (genets, mongooses, squirrels) but for simplicity we refer to them as species.

We followed common recommendations on sampling a wide area to capture far-ranging species and using many CT stations for long periods (O'Brien et al., 2010; Tobler et al., 2008). However, our mixed design for CT station placement over several years demands caution in interpreting differences in species richness between PAs. Differential use of wildlife trails could bias for and against some species and individuals (Harmsen et al., 2009; Larrucea et al., 2007; Maffei et al., 2004). Also the multi-year span of the study could confound temporal changes in species richness (turnover, colonization, local extinction, etc.) with differences between PAs.

Because we did not resample the same CT stations at successive seasons and within-seasons, we have no objective way to define resampling intervals. Hence our design did not meet the demands of occupancy analysis for two key reasons. First, robust and precise estimation of occupancy demands an appropriate model of detection probability as a prerequisite (Bailey et al., 2007). Our “model of detection probability” (which we call detectability) is based on rank correlations (i.e., relative between species) not an absolute probability of detection. Furthermore our data contain neither temporal replication between-seasons nor objective criteria for within-season replication, yet “occupancy estimators were generally less biased under designs that include temporal survey replication both within and among seasons...” (emphasis added, p. 289 Bailey et al., 2007). Although we might adopt an arbitrary interval to designate a temporal replicate, that could be biased by variable likelihood of photo-capture over time, e.g., trap shyness (Wegge et al., 2004). Our results on detectability can guide future efforts

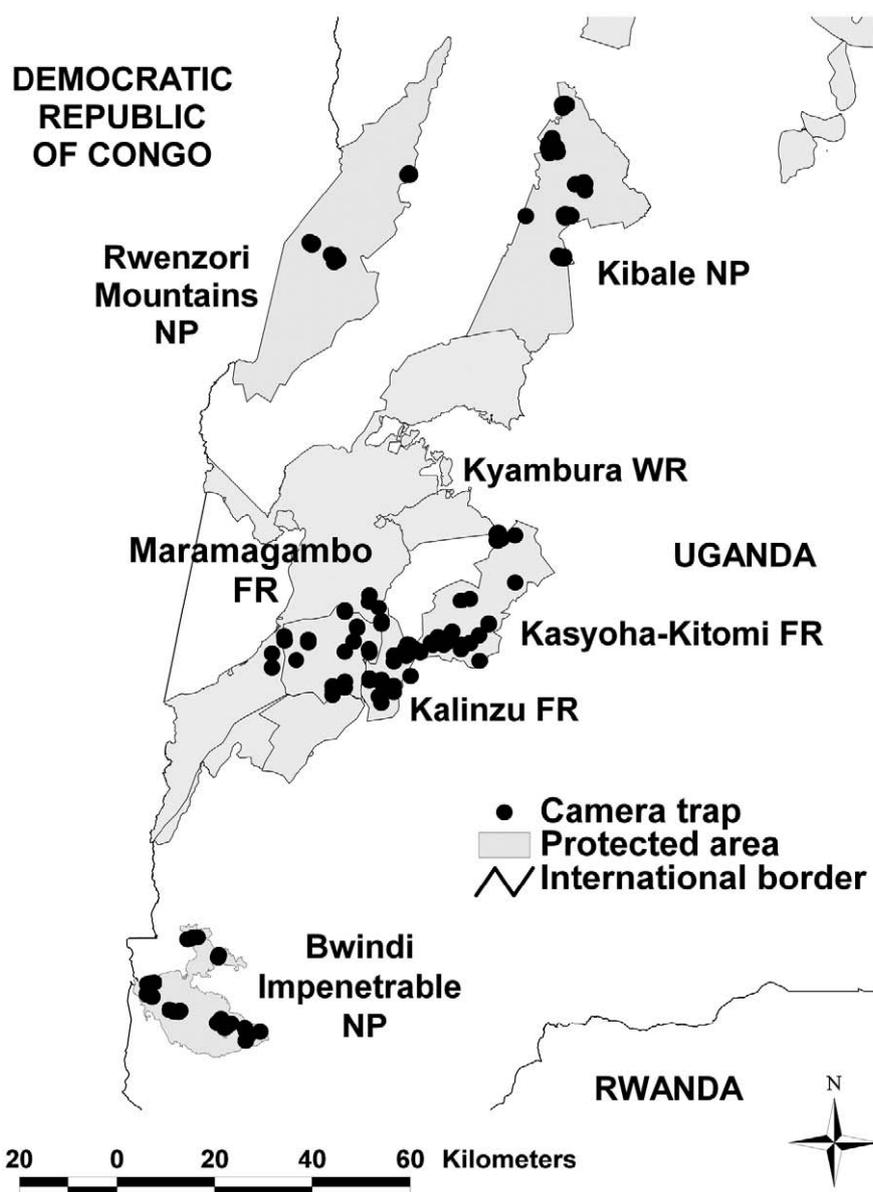


Fig. 1. Western Ugandan protected areas sampled with camera traps (dark circles).

Table 1
Wildlife photo-captured in seven protected areas of western Uganda 2004–2008.

Protected area (km ²) ^a	N of independent				Species richness		Abundance indices		
	Trap-days	Localities	CT stations	Photo-captures (wildlife)	Observed	As % of total	Humans/100 trap-days ^b	Species/100 trap-days	Photo-captures/100 trap-days
Bwindi NP (321)	864	5	28	225	18	50	46.875	2.083	26.042
Kalinzu FR (137)	1498	1	23	101	7	19	0.334	0.467	6.742
Kasyoha–Kitomi FR (399)	2345	6	49	141	20	56	2.4733	0.853	6.013
Kibale NP (764)	1318	5	45	313	19	53	5.083	1.442	23.748
Kyambura WR (157)	602	2	12	39	10	28	1.163	1.661	6.478
Maramagambo FR (580)	893	1	25	92	17	47	1.904	1.904	10.302
Rwenzori NP (996)	1321	3	10	37	5	14	1.363	0.379	2.801
Total	8841	23	192	948	36	100			

^a NP = National Park, WR = Wildlife Reserve, FR = Forest Reserve.

^b Includes domestic animals with or without humans and sums individuals in all photos.

to estimate detection probabilities but that will require resampling our sites. Therefore we limit ourselves to two sets of analyses relating to photo-capture rates and interspecific variation in detectability.

2.1. Photo-capture rates

We report estimates of observed species richness and proportional species richness as a percentage of the total species inven-

tory for the study. We also report the number of CT stations, localities, and PAs at which a species was photographed as indices of relative distribution over the landscape. To index relative abundance, we follow (O'Brien et al., 2003) and calculate independent photos per 100 CT station-days (RAI_2) with one difference. We do not have records of time (only date) on our photos, so we defined photos to be independent when taken of the same species in the same CT station on different days. Thus any large group passing a CT station multiple times in 1 day would still be recorded as one independent photo no matter how many other species were interspersed or how many animals were photographed. This is more conservative than the latter authors' criterion of 0.5 h between successive photos of the same species or interspersed of different species. It should be noted that mixed-species associations including terrestrial forms such as baboons, L'hoest's monkeys, duikers, bushpigs, and guinea fowl are not uncommon in these forests (Struhsaker, 1997; Treves, 1997; Waser, 1987). Therefore we explored detectability by analyzing the associations between species characteristics on the one hand and RAI_2 and the indices of spatial distribution on the other hand.

2.2. Detectability

We collated species data on MASS (natural log of female body mass), RANGE (natural log of female home range size), and categorized species' habitat specialization HABITATS as t , f , or $t + f$, where t = primarily terrestrial travelers vs. arboreal, volant, or semi-aquatic travelers, and f = species found at higher densities in forests or woodlands than more open habitats, all from (Dorst and Dandelot, 1993; Estes, 1991) and personal observations of the authors. We also used the mean and maximum observed group sizes from our photos (GROUPMEAN and GROUPMAX respectively). Note that large-bodied animals might have had smaller average values when calculated this way because fewer can fit in one photographic frame but we found no such correlation in our dataset (our measures of gregariousness vs. female mass: $r_s < 0.05$, $P > 0.80$ in both tests).

For the categorical predictor of habitat specializations (HABITATS) we employed the non-parametric median test with chi-squared approximation and $df = 2$. For the four continuous predictors (MASS, RANGE, GROUPMEAN, and GROUPMAX) we employed the Spearman rank correlation coefficient. The indices of abundance and the count data of number of photos violated the assumption of constant variance for linear correlations so we ran non-parametric statistics in JMP 8 (SAS Institute 2009). We accepted $\alpha \leq 0.04$ to correct for the 25 tests we ran.

3. Results

3.1. Species richness, abundance, and inventories

In 8841 CT station-days we collected 1750 useful photographs. Setting aside 335 photos of humans or domestic animals, the remaining 1415 contained 948 (67%) independent photos of 36 wildlife species. Cameras detected 5–20 species per PA or 14–56% of the total pool (Table 1). NPs and Reserves did not differ in total number of humans photo-captured, number of wildlife species photo-captured, or independent photos, all divided by CT-days ($df = 1$, $X^2 < 1.1$, $P > 0.30$ for all tests).

We photo-captured the greatest number of species at Kasyoha-Kitomi, but Kibale, Bwindi, and Maramagambo yielded almost as many with less effort (Table 1). RAI_2 of all wildlife at PAs varied from 2.8–26.0 (Table 1), with Kibale and Bwindi NPs having 2–3 times the relative abundances of the Reserves. Rwenzori NP approximated one-third of the abundances of the Reserves (Ta-

ble 1). We fitted an exponential curve to the number of species photo-captured at a PA against the number of CT-days and found that after about 1000 CT-days and 18 species, the detection of new species approached an asymptote. Therefore we probably under-estimated species richness at Kyambura with only 12 species, and possibly Bwindi and Maramagambo with 18 and 17 species respectively (for a warning against asymptote-fitting, see O'Brien, 2008).

The most diverse groups photo-captured were the eight genera of carnivores, five genera of non-human primates, and eight genera of ungulates or megaherbivores, which included 6–7 species of duikers (Table 2, Appendix 1). The most commonly photo-captured species in the NPs were all duikers: yellow-backed (Bwindi), red (Kibale, species indeterminate), and black-fronted (Rwenzori). The single photo of a red-flanked duiker may have been an old individual of black-fronted duiker (Plumptre, unpublished data), so we omit further discussion of it. By contrast, olive baboons were the most commonly photo-captured species at all four Reserves. Cameras in the NPs detected eight species not detected at the Reserves (great blue turaco, helmeted guineafowl, handsome francolin, African white-bellied pangolin, red duiker, redbellied monkey, Rwenzori duiker, and African wild cat), whereas cameras in Reserves detected seven species not detected in the NPs (black-and-white colobus, giant forest hog, hippopotamus, leopard, spotted hyaena, squirrels, and waterbuck; Table 2).

Species varied in spatial distribution. They were detected at 1–58 CT stations, 1–23 localities, and 1–6 PAs. Baboons and L'hoest's monkeys were the most widespread. Different species were photo-captured 1–230 times (mean 39, sd 56) with 1–119 independent photos per species (mean 27, sd 37). RAI_2 values for species varied from 0.05 to 6.22 (mean 0.72, sd 1.15) independent photos per 100 CT-days.

Species varied in gregariousness. The largest groups photo-captured were helmeted guineafowl (up to nine) and olive baboons (up to six). Fifteen other species were photographed in pairs or trios (Table 2).

3.2. Detectability

The total number of photos we obtained of a species was highly correlated to the indices of abundance and spatial distribution: RAI_2 , and the numbers of CT sites, localities, and PAs at which that species was detected ($r_s = 0.87, 0.96, 0.91$, and 0.71 respectively; $P < 0.0001$ in every case). GROUPMAX was significantly, positively correlated with all the photo-capture measures whereas GROUPMEAN was associated with RAI_2 only (Table 3). Species with GROUPMAX > 1 had significantly higher RAI_2 than those with GROUPMAX of 1 ($df = 1$, $X^2 = 13.1$, $P = 0.0003$). HABITATS predicted RAI_2 , and the numbers of CT stations and localities at which a species was photo-captured. All the significant relationships were in the predicted direction.

An anonymous reviewer suggested our method may underestimate the abundance of territorial, solitary species with our conservative criterion for independence between photos. For example if we unwittingly placed cameras near the boundaries of small territories (e.g., paths), we might have discarded numerous photos of different individuals visiting an area of overlap between their ranges, on the same day. We tested this prediction *post hoc* by calculating the number of photos discarded (total photos – independent photos) and testing if that number differed between species photo-captured in groups or solitary. The result was significant ($df = 1$, $X^2 = 6.9$, $P = 0.009$) but in the direction opposite to that predicted; namely we discarded more photos of gregarious species (22 sd 31 vs. 4 sd 8 photos discarded on average)–suggesting a less conservative approach would have further inflated the photo records of gregarious species.

Table 2
Wildlife species photo-captures and characteristics.

Wildlife ^a	Protected areas ^b	CT stations (localities)	Total photos	Independent photos	RAI ₂ ^c	Group size mean (range)	MASS (kg)	RANGE (km ²)	HABITATS ^f
Baboon, olive	Bw, Ka ^b , Kk ^b , Ki, Ky ^b , Ma ^b	58 (23)	230	119	1.58	1.5 (1–6)	11.5	22.0	t, f
Black-and-white colobus	Kk, Ky	4 (3)	6	4	0.14	1.2 (1–2)	8.3	0.2	f
Black-fronted duiker	Bw, Kk, Rw ^b	30 (6)	118	101	1.73	1 (1–2)	13.9	na	t, f
Blue duiker	Ka, Kk, Ki, Ma	41 (17)	140	111	1.83	1 (1–3)	4.9	0.1	t, f
Blue monkey	Ka, Kk, Ki, Rw	4 (4)	6	4	0.05	1 (1)	4.0	0.2	f
Buffalo, cape	Ki, Ma	2 (2)	3	2	0.09	1 (1)	576.0	10.5	t
Bushbuck	Ka, Kk, Ki, Ma	24 (15)	72	50	0.83	1.1 (1–2)	42.5	0.0	t, f
Bushpig	Bw, Ka, Kk, Ki, Ma	24 (11)	44	30	0.43	1.2 (1–3)	70.0	5.1	t, f
Chimpanzee	Bw, Ka, Kk, Ki, Ky, Ma	45 (15)	104	76	1.01	1.2 (1–3)	38.0	3.0	t, f
Civet, African	Bw, Ki, Ma	10 (6)	18	15	0.49	1 (1)	13.5	na	t, f
Elephant	Bw, Kk, Ki, Ky, Ma	22 (13)	129	45	0.75	1.1 (1–3)	3250	1757	t
Gambian rat	Ka, Kk, Ki, Ky	8 (6)	12	9	0.16	1 (1)	1.0	na	t, f
Genets	Kk, Ki, Ky, Ma	9 (7)	14	11	0.21	1 (1)	1.8	2.6	f
Giant forest hog	Ma	2 (1)	4	3	0.34	1.3 (1–2)	180.0	na	t, f
Golden cat, African	Bw, Kk, Ki, Ma	11 (6)	13	12	0.22	1 (1)	6.2	na	t, f
Great blue turaco	Ki	1 (1)	3	2	0.15	1.3 (1–2)	1.0	na	f
Guinea fowl, helmeted	Bw, Ki	19 (11)	42	28	1.28	2.4 (1–9)	1.1	na	t, f
Handsome francolin	Bw	4 (3)	16	13	1.51	1.3 (1–3)	1.0	na	t, f
Hippopotamus	Kk, Ky, Ma	7 (5)	26	20	0.52	1.1 (1–2)	1400	na	t
L'hoest's monkey	Bw, Kk, Ki, Ma, Rw	55 (17)	127	91	1.13	1.1 (1–3)	3.5	na	t, f
Leopard	Ma	2 (1)	2	2	0.22	1 (1)	43.0	17.5	t, f
Mongoose ^d	Bw, Kk, Ki, Ky, Rw	7 (7)	11	9	0.12	1 (1)	2.7	3.4	t, f
Mountain gorilla	Bw	4 (2)	8	4	0.46	1.5 (1–3)	85.0	6.0	t, f
Pangolin, African white-bellied	Bw	1 (1)	1	1	0.12	1 (1)	2.5	na	t, f
Red duiker	Ki ^b	26 (13)	109	82	6.22	1 (1)	13.6	0.1	t, f
Red-flanked duiker ^e	Bw	1 (1)	1	1	0.12	1 (1)	12.5	na	t, f
Redtail monkey	Ki	1 (1)	1	1	0.08	1 (1)	2.0	0.2	f
Rwenzori duiker	Rw	1 (1)	2	2	0.08	1 (1)	15.0	na	t, f
Serval	Kk, Ki	2 (2)	3	2	0.06	1 (1)	11.0	15.5	t, f
Side-striped jackal	Bw, Kk, Ky	8 (5)	9	9	0.24	1 (1)	8.3	2.5	t
Spotted hyena	Ma	1 (1)	1	1	0.11	1 (1)	71.0	30.0	t
Squirrel spp.	Kk	3 (2)	4	4	0.17	1.3 (1–2)	1.0	na	f
Waterbuck	Ma	1 (1)	1	1	0.11	1 (1)	186.0	6.0	t
Weyn's duiker	Bw, Kk, Ky, Ma	15 (8)	17	16	0.34	1.1 (1–2)	15.0	na	t, f
Wild cat, African	Bw	1 (1)	1	1	0.12	1 (1)	4.0	0.8	t
Yellow-backed duiker	Kk, Bw ^b	25 (8)	116	92	2.87	1 (1)	68.0	na	t, f

^a One unknown species (blurry photo) excluded; Scientific names in Appendix 1.

^b Bw = Bwindi, Ka = Kalinzu, Kk = Kasyoha–Kitomi, Ki = Kibale, Ky = Kyambura, Ma = Maramagambo, Rw = Rwenzori, identifies the species-PA pairs that were most common (most independent photos).

^c Independent photos per 100 CT-days.

^d Two species identified plus one unidentified.

^e Possibly an old black-fronted duiker.

^f Mainly terrestrial = t, higher densities in forest or woodlands = f, see Methods for criteria.

HABITATS did not show constant variance against RAI₂ ($F = 5.8$, $df = 2$, 13.7 , $P < 0.015$) and the residual plots for GROUPMAX and GROUPMEAN appeared heteroschedastic, so we did not attempt multivariate linear analysis. When we set aside the non-terrestrial (semi-aquatic, volant, and arboreal) travelers, GROUPMAX and GROUPMEAN were still strongly correlated to RAI₂ ($n = 28$, $r_s = 0.61$ and 0.51 , $P < 0.0031$ in both cases) suggesting microsite preferences did not confound the association with gregariousness.

Finally, to assess rarity in the landscape we used our most conservative measure of spatial distribution (number of PAs in which a species was photo-captured), discarded non-terrestrial travelers and used RAI₂ to index abundance (Table 4). We also omitted species groups (mongooses, genets) because we felt conclusions about their rarity were premature without specific resolution. Six species were localized in 1–2 PAs and in the lowest quartile for RAI₂, and another three had intermediate abundances but were localized in 1–2 PAs (Table 4).

4. Discussion

We found several species-specific characteristics associated with the number of photos and the number of sites at which a species was detected. Thus we are building upon prior work that showed detectability varying with species traits and behavioral

ecology (Larrucea et al., 2007; Long et al., 2007; O'Brien et al., 2003; Tobler et al., 2008). Prior work showed how detection probability can confound estimates of abundance and spatial distribution made from camera-trap photos. For example, non-breeding, younger coyotes, *Canis latrans*, were more detectable than others and detectability of the same age–sex classes even varied by season and microsite (Larrucea et al., 2007). Between species, detectability was higher for habitat generalists, terrestrial forms, and large-bodied species (O'Brien et al., 2003; Tobler et al., 2008). Microsite use was only weakly associated with relative abundance between species in our study, probably because few non-terrestrial species appeared in our pool. We did not find female body mass or female range size associated with abundance or distribution but these variables taken from the literature were crude and may not have adequately differentiated the populations within our landscape. By contrast, gregariousness indexed as the mean or maximum group size in our photos was strongly correlated with relative abundance and the indices of distribution.

There are two possible interpretations of the latter finding. First, species observed in groups of two or more might be found at higher densities than ones photographed singly across most of our sites. Consistent with this, all carnivores from genets to hyenas were photo-captured alone (Table 2) and carnivores generally occur at low densities because of their diet. But gregarious species

Table 3
Univariate tests of detectability.

Wildlife characteristics ^a	Test ^b	RAI ₂	CT stations ^c	Localities ^c	PAs ^c
HABITATS	χ^2	8.2	7.3	8.6	1.7
	<i>P</i>	0.017	0.026	0.013	0.428
GROUPMAX	r_s	0.62	0.53	0.51	0.35
	<i>P</i>	<0.0001	0.0009	0.0013	0.038
GROUPMEAN	r_s	0.49	0.33	0.30	0.15
	<i>P</i>	0.0023	0.053	0.076	0.395
MASS	r_s	0.11	0.07	0.00	0.03
	<i>P</i>	0.521	0.708	0.991	0.877
RANGE	r_s	-0.10	-0.16	-0.18	0.09
	<i>P</i>	0.664	0.495	0.458	0.704

^a Definitions in Methods and Table 2.
^b Median test ($df = 2$) or Spearman rank correlation ($n = 36$ except for RANGE $n = 20$ and HABITATS $n = 35$).
^c Definitions in Methods and Table 1.

widely considered rare or in low-density populations (chimpanzee, elephant, giant forest hog, hippopotamus, L'hoest's monkey, mountain gorilla) produced estimates of relative abundances above the observed median of 0.23. A more likely explanation is that the index of relative abundance was inflated for gregarious species. This inflation could arise from repeated photo-capture at the same camera-trap stations. Indeed we found more photos of gregarious species in the same day (discarded from analyses) and across multiple days at the same camera-trap stations or different ones (Table 3). In sum, gregarious species appeared to revisit camera traps more than species photographed as singletons and gregarious species also appeared more widespread or having larger ranges. We recommend further research into detection probabilities of gregarious animals, using marked or known individuals to estimate the functional relationship between different group sizes, ranging patterns, and independence of recapture intervals. We also recommend adoption of a more conservative interval than 30 min between photos of the same species at a given camera-trap station.

Because we found significant differences in relative abundance for species with maximum group sizes of two or more, we believe this potential bias is widespread. Interindividual proximity and even overlap in range use will vary by species, season, site, and individual even among "solitary" species (Harmsen et al., 2009). Because gregariousness varies by numbers and proximity of kin, mates, and other associates, we encourage additional study of gregariousness and range overlap before estimating abundance of wild animals without individual identification. For capture-recapture theory, the predominant software (CAPTURE) assumes individual variation and temporal variation have independent effects on capture probabilities (Otis et al., 1978). We predict several common features of groups as small as two animals violate that

assumption. If the probability that an individual joins a group varies among groups (by size, location, season, etc.) and among individuals (by rank, sex, dominance, etc.) then individual and temporal variation in capture probabilities will not be independent but rather strongly interacting. A number of primate, carnivore, and ungulate groups fuse, split, and change as individuals come and go in relation to changing costs and benefits of association and resource availability (Chapman et al., 1995; Larrucea et al., 2007; Waser and Wiley, 1979; Wrangham et al., 1993). Males and females, adults and young, or dominants and subordinates often differ in their propensity to associate and travel in groups. Hence the probability of capture at a given camera is a function of group size and composition, individual traits, and time, all interacting in a complex manner. Chimpanzees epitomize this variability but baboons, elephants, and pigs may also. Studies of highly solitary animals, such as jaguars and tigers, may not be as strongly affected by this bias (Harmsen et al., 2009; Karanth and Nichols, 1998; Maffei et al., 2004; Mccarthy et al., 2008), except when traveling with mates or dependent young. But other species such as pack-living predators and the gregarious prey of solitary carnivores may be acutely affected by the bias. Further empirical and modeling studies will be needed to quantify the effect.

Our finding of higher detectability among gregarious species has theoretical implications for predator-prey ecology as well. Larger groups should not be assumed safer *a priori* (Bednekoff and Lima, 1998; Treves, 2000). Gregarious species may be detected more often by sit-and-wait predators, just as they were detected more often by our camera traps. If larger groups can also be followed more easily than singletons, a stalking predator would benefit from waiting for prey stimuli and following them until an unwary group member can be approached.

4.1. Species richness and conservation status

The western Ugandan national parks, Bwindi and Kibale, contained higher abundances of forest-woodland wildlife captured in fewer camera-trap days than did the four Reserves (Table 1). This suggests better habitats, better protections, or larger areas. However Bwindi was smaller than three of the four reserves, hence area seems inadequate to explain the abundances seen in the two national parks. Examining protection, the frequency of photo-captures of humans was not different between the national parks and the reserves but high rates of photo-capture of tourists and researchers in the former may obscure the disparate threats posed by different groups of people. We could not assess habitat quality. Differential gregariousness did not create the apparent differences between national parks and reserves either, because the most common species in the former were the mostly solitary duikers whereas the most commonly photo-captured species in the Reserves were the gregarious baboons.

Table 4
Relative abundance and distribution of forest-woodland wildlife in protected areas of western Uganda.

Relative abundance RAI ₂ ^a	Spatial distribution	
	Localized: 1–2 PAs	Widespread: 3–6 PAs
Abundant (top quartile)	Red duiker, yellow-backed duiker, handsome francolin ^c , helmeted guineafowl ^c	Blue duiker ^c , black-fronted duiker ^c , olive baboon ^c
Intermediate (interquartile range)	Mountain gorilla ^{b,c} , giant forest hog ^c , leopard	l'hoest's monkey ^{b,c} , chimpanzee ^{b,c} , bushbuck ^c , elephant ^c , African civet, bushpig ^c , Weyn's duiker ^c , side-striped jackal, African golden cat, gambian rat
Rare (lowest quartile)	African wild cat, spotted hyena, waterbuck, cape buffalo, Rwenzori duiker, serval	–

^a Non-terrestrial travelers, genets, mongooses, and red-flanked duiker were omitted (see Results).
^b Vulnerable by IUCN (2008).
^c GROUPMAX > 1.

The national parks lacked a few species that were present in one or more reserves and vice versa (Table 2). This leads us to two conclusions regarding protected area conservation in this landscape. First, national parks and reserves are not interchangeable; both types are needed for conservation of large mammal and terrestrial bird diversity. Second, cameras in the woodland reserves may have captured species that rarely use the more densely forested sites such as Bwindi and Kibale (e.g., hippopotamus, serval, side-striped jackal, spotted hyaena, waterbuck). We return to the carnivores below but buffaloes and waterbucks are found in great numbers in savanna parks (Rwetsiba, 2005; Treves et al., 2009), so their rarity in our study does not demand conservation action. Preference for less forested habitats does not explain why we did not detect black-and-white colobus or squirrels in the national parks, as these are present and seemingly abundant (personal observations; Struhsaker, 1997). Most likely their arboreality reduced their detectability.

Incorporating gregariousness into our assessments of rarity of different species (Table 4), we found cause for concern about the conservation status of several species. Six species were least abundant and narrowly localized in the landscape (African wild cat, spotted hyaena, waterbuck, Cape buffalo, Rwenzori duiker, and serval). As noted above, waterbuck and Cape buffalo are more abundant in nearby savanna parks (Rwetsiba, 2005). The same may be true for servals, side-striped jackals, and African wild cats (all listed as “Least concern” (IUCN, 2008), but we recommend Ugandan wildlife authorities support surveys for them to assess whether savanna parks protect adequate populations of these carnivores.

On the other hand, the Rwenzori duiker is recognized by some as a distinct species allied to *Cephalophus nigrifrons* and found only in the Rwenzori Mountains above 2500 m altitude (IUCN, 2008; Plumtre et al., 2009). It may therefore be an endemic with a very restricted range, deserving national and global conservation attention.

Finally, three species showed intermediate abundances but were found in only 1–2 PAs (Table 4): leopards, giant forest hogs, and mountain gorillas. The mountain gorilla is listed as “Critically Endangered” (IUCN, 2008) and already receiving focused conservation attention. The giant forest hog uses forested habitats as its name would imply as well as more open savanna–woodland and is gregarious (Estes, 1991). Therefore we recommend Ugandan wildlife officials support a focused survey that includes savanna areas to determine if the rarity we observed is real or biased by low detectability.

Our data also suggest large carnivores need more conservation attention. Leopards and spotted hyaenas were almost eradicated from Uganda in the 20th century (Treves and Naughton-Treves, 1999), and appear not to have recovered strongly. Spotted hyaenas have been reduced in number in the savanna parks because of poisoning by cattle keepers who use the parks illegally. We recommend a survey to assess their status throughout western Uganda. The leopard demands more urgent conservation action. Leopards were recently reclassified from “Least Concern” to “Near Threatened” globally, with a decreasing population trend (IUCN, 2008). Across Africa, leopards occur in all habitats except desert (Bailey, 1993; Estes, 1991; Henschel and Ray, 2003), but we detected 1–2 in Maramagambo Forest Reserve only. One has been seen recently crossing a road in Kibale NP (C. Chapman, personal communication 2009), yet we did not detect them in woodland or forested areas of national parks at all. It seems unlikely our cameras simply missed leopards given the intensity of effort (Balme et al., 2009; Henschel and Ray, 2003). Comparison with its smaller relative, the African golden cat, corroborates that view. One would expect the golden cat to be as difficult to detect by camera trapping as the leopard or more difficult because of its rarity in other places,

solitary habits, and higher arboreality (Boy, 2003; Henschel and Ray, 2003; IUCN, 2008; Ray et al., 2005). Yet we photo-captured golden cats 13 times in four PAs (Table 2). Thus, the scarcity of leopards in the Greater Virunga landscape seems to be a robust result, which emphasizes the need for leopard conservation in western Uganda. Large carnivores often suffer higher mortality near the edges of protected areas, leading to local extinction from small ones (Balme et al., in press; Loveridge et al., 2007; Woodroffe and Ginsberg, 1998). Therefore recent policies allowing trophy hunting of leopards in Uganda (www.cites.org/common/cop/14/inf/E14i-22.pdf) seem imprudent in our study area (see also Balme et al., 2009, 2010).

Acknowledgments

The manuscript was improved by comments from T. O'Brien, L. Hunter, T. Jones, R. Zug and two anonymous reviewers.

Appendix A

See Table A1.

Table A1
Scientific names of wildlife species from IUCN 2008.

Common name	Scientific name
Baboon	<i>Papio anubis</i>
Black-and-white colobus	<i>Colobus guereza</i>
Black-fronted duiker	<i>Cephalophus nigrifrons</i>
Blue duiker	<i>Philantomba monticola</i>
Blue monkey	<i>Cercopithecus mitis</i>
Buffalo	<i>Syncerus caffer</i>
Bushbuck	<i>Tragelaphus scriptus</i>
Bushpig	<i>Potamochoerus larvatus</i>
Chimpanzee	<i>Pan troglodytes</i>
African civet	<i>Civettictis civetta</i>
Elephant	<i>Loxodonta africana</i>
Gambian rat (Northern giant pouched rat)	<i>Cricatomys gambianus</i>
Genets	<i>Viverridae</i> spp.
Giant forest hog	<i>Hylochoerus meinertzhageni</i>
Golden cat	<i>Caracal aurata</i>
Great blue turaco	<i>Corythaeola cristata</i>
Helmeted guineafowl	<i>Numida meleagris</i>
Handsome francolin	<i>Francolinus nobilis</i>
Hippopotamus	<i>Hippopotamus amphibius</i>
L'hoest's monkey	<i>Cercopithecus lhoesti</i>
Leopard	<i>Panthera pardus</i>
Mongoose ^a	<i>Herpestidae</i> spp.
Mountain gorilla	<i>Gorilla beringei</i>
African white-bellied pangolin	<i>Phataginus tricuspis</i>
Red duiker	<i>Cephalophus</i> spp? or <i>Sylvicapra grimmia</i>
Red-flanked duiker	<i>Cephalophus rufilatus</i>
Redtail monkey	<i>Cercopithecus ascanius</i>
Rwenzori duiker	<i>Cephalophus rubidus</i>
Serval	<i>Leptailurus serval</i>
Side-striped jackal	<i>Canis adustus</i>
Spotted hyaena	<i>Crocuta crocuta</i>
Squirrel spp.	<i>Sciuridae</i>
Waterbuck	<i>Kobus ellipsiprymnus</i>
Weyn's duiker	<i>Cephalophus weynsi</i>
Wild cat	<i>Felis silvestris</i>
Yellow-backed duiker	<i>Cephalophus silvicultor</i>

^a Two identified but one unidentified.

References

- Bailey, L.L., Hines, J.E., Nichols, J.D., Mackenzie, D.I., 2007. Sampling design trade-offs in occupancy studies with imperfect detection: examples and software. *Ecological Applications* 17, 281–290.
- Bailey, T.N., 1993. *The African Leopard: Ecology and Behavior of a Solitary Felid*. Columbia University Press, New York.

- Balme, G., Hunter, L.T.B., Slotow, R., 2009. Evaluating methods for counting cryptic carnivores. *Journal of Wildlife Management* 73, 431–443.
- Balme, G., Slotow, R., Hunter, L., in press. Edge effects and the impact of non-protected areas in carnivore conservation: leopards in the Phinda-Mkhuzi Complex, South Africa. *Animal Conservation*.
- Balme, G.A., Hunter, L.T.B., Goodman, P., Ferguson, H., Craigie, J., Slotow, R., 2010. An adaptive management approach to trophy hunting of leopards *Panthera pardus*: a case study from KwaZulu-Natal, South Africa. In: Macdonald, D., Loveridge, A.J. (Eds.), *Biology and Conservation of Wild Felids*. Oxford University Press, Oxford.
- Bednekoff, P.A., Lima, S.L., 1998. Re-examining safety in numbers: Interactions between risk dilution and collective detection depend upon predator targeting behaviour. *Proceedings of the Royal Society of London Series B* 265, 2021–2026.
- Boinski, S., Garber, P., 2000. *On the Move: How and Why Animals Travel in Groups*. University of Chicago Press, Chicago.
- Boy, G., 2003. Phantom Feline. *SWARA* April–June, pp. 26–43.
- Chapman, C.A., Wrangham, R.W., Chapman, L.J., 1995. Ecological constraints on group size: an analysis of spider monkey and chimpanzee subgroups. *Behavioral Ecology and Sociobiology* 36, 59–70.
- Dorst, J., Dandelot, P., 1993. *Larger Mammals of Africa*. Harper Collins, London.
- Estes, R.D., 1991. *The Behavior Guide to African Mammals*. The University of California Press, Berkeley, CA.
- Field, S., Tyre, A., Possingham, H., 2005. Optimizing allocation of monitoring effort under economic and observational constraints. *Journal of Wildlife Management* 69, 473–482.
- Gompper, M.E., Kays, R.W., Ray, J.C., Lapoint, S.D., Bogan, D.A., Cryan, J.R., 2006. A comparison of noninvasive techniques to survey carnivore communities in northeastern North America. *Wildlife Society Bulletin* 34, 1142–1151.
- Harmsen, B.J., Foster, R.J., Silver, S.C., Ostro, L.E.T., Doncaster, C.P., 2009. Spatial and temporal interactions of sympatric jaguars (*Panthera onca*) and pumas (*Puma concolor*) in a neotropical forest. *Journal of Mammalogy* 90, 612–620.
- Henschel, P., Ray, J.C., 2003. *Leopards in African Rainforests: Survey and Monitoring Techniques*. Wildlife Conservation Society, Global Carnivore Program, NY.
- Howard, P., 1991. *Nature Conservation in Uganda's Tropical Forest Reserves*. International Union for the Conservation of Nature, Gland.
- IUCN, 2008. *Red List*. International Union for the Conservation of Nature, Gland, Switzerland.
- Karanth, K.U., Nichols, J.D., 1998. Estimation of tiger densities in India using photographic captures and recaptures. *Ecology* 79, 2852–2862.
- Karanth, K.U., Nichols, J.D., Kumar, N.S., Link, W.A., Hines, J.E., 2004. Tigers and their prey: predicting carnivore densities from prey abundance. *Proceedings of the National Academy of Sciences USA* 101, 4854–4858.
- Larrucea, E.S., Brussard, P.F., Jaeger, M.M., Barrett, R.H., 2007. Cameras, coyotes, and the assumption of equal detectability. *Journal of Wildlife Management* 71, 1682–1689.
- Long, R.A., Donovan, T.M., Mackay, P., Zielinski, W.J., Buzas, J.S., 2007. Comparing scat detection dogs, cameras, and hair snares for surveying carnivores. *Journal of Wildlife Management* 71, 2018–2025.
- Loveridge, A.J., Searle, A.W., Murindagomo, F., MacDonald, D.W., 2007. The impact of sport-hunting on the population dynamics of an African lion population in a protected area. *Biological Conservation* 134, 548–558.
- Maffei, L., Cuellar, E., Noss, A., 2004. One thousand jaguars (*Panthera onca*) in Bolivia's Chaco? Camera trapping in the Kaa-lyá National Park. *Journal of Zoology* 262, 295–304.
- Manley, P.N., Zielinski, W.J., Schlesinger, M.D., Mori, S.R., 2004. Evaluation of a multiple-species approach to monitoring species at the ecoregion scale. *Ecological Applications* 14, 296–310.
- Mccarthy, K.P., Fuller, T.K., Ming, M., Mccarthy, T.M., Waits, L., Jumabaev, K., 2008. Assessing estimators of snow leopard abundance. *Journal of Wildlife Management* 72, 1826–1833.
- O'Brien, T.G., 2008. On the use of automated cameras to estimate species richness for large- and medium-sized rainforest mammals. *Animal Conservation* 11, 179–181.
- O'Brien, T.G., Kinnaird, M.F., Wibisono, H.T., 2003. Crouching tigers, hidden prey: Sumatran tiger and prey populations in a tropical forest landscape. *Animal Conservation* 6, 131–139.
- O'Brien, T.G., Kinnaird, M.F., Wibisono, H.T., 2010. Estimation of species richness of large vertebrates using camera traps: an example from an Indonesian rainforest. In: O'Connell, A., Nichols, J., Karanth, K.U. (Eds.), *Camera Traps: Methods and Analyses*. Springer Verlag Press, New York.
- Otis, D.L., Burnham, K.P., White, G.C., Anderson, D.R., 1978. Statistical inference from capture data on closed populations. *Wildlife Monographs* 62, 1–135.
- Plumptre, A.J., Davenport, T.R.B., Behangana, M., Kityo, R., Eilu, G., Ssegawa, P., Ewango, C., Meirte, D., Kahindo, C., Herremans, M., Peterhans, J.K., Pilgrim, J.D., Wilson, M., Languy, M., Moyer, D., 2007a. The biodiversity of the Albertine Rift. *Biological Conservation* 134, 178–194.
- Plumptre, A.J., Kujirakwinja, D., Treves, A., Owijuni, I., Rainer, H., 2007b. Transboundary conservation in the Greater Virunga landscape. *Biological Conservation* 134, 279–287.
- Plumptre, A.J., Kujirakwinja, D., Nampindo, S., 2009. Conservation of Landscapes in the Albertine Rift. In: Redford, K.H., Grippio, C. (Eds.), *Protected Areas, Governance and Scale*. WCS Working Paper, Bronx, NY, pp. 27–34.
- Ray, J.C., Hunter, L., Zigoris, J., 2005. Setting conservation and research priorities for larger African carnivores. In: *Wildlife Conservation Society Working Papers #24*, Wildlife Conservation Society, Bronx, NY, pp. 1–19.
- Robinson, J.G., 1986. Seasonal variation in use of time and space by the wedge-capped capuchin monkeys, *Cebus olivaceus*: implications for foraging theory. *Smithsonian Contributions to Zoology* 431, 1–59.
- Rwetsiba, A., 2005. *Wildlife Population Trends in Uganda, 1960–2005*. Uganda Wildlife Authority, Kampala, Uganda.
- van Schaik, C.P., Griffiths, M., 1996. Activity patterns of Indonesian rain forest mammals. *Biotropica* 28, 105–112.
- Silver, S.C., Ostro, L.E.T., Marsh, L.K., Maffei, L., Noss, A.J., Kelly, M.J., Wallace, R.B., Gomez, H., Ayala, G., 2004. The use of camera traps for estimating jaguar *Panthera onca* abundance using capture/recapture analysis. *Oryx* 38, 148–154.
- Struhsaker, T.T., 1997. *Kibale: A Case Study of Logging in a Tropical Rainforest*. University of Florida Press, Gainesville, FL.
- Thomas, L., Laake, J.L., Strindberg, S., Marques, F.F.C., Buckland, S.T., Borchers, D.L., Anderson, D.R., Burnham, K.P., Hedley, S.L., Pollard, J.H., Bishop, J.R.B., Marques, T.A., 2006. *Distance 5.0*. University of St Andrews, Research Unit for Wildlife Population Assessment.
- Tobler, M.W., Carrillo-Percastegui, S.E., Pitman, R.L., Mares, R., Powell, G., 2008. An evaluation of camera traps for inventorying large- and medium-sized terrestrial rainforest mammals. *Animal Conservation* 11, 169–178.
- Treves, A., 1997. *Self-Protection in Primates*. Harvard University, Cambridge, MA.
- Treves, A., 2000. Theory and method in studies of vigilance and aggregation. *Animal Behaviour* 60, 711–722.
- Treves, A., Naughton-Treves, L., 1999. Risk and opportunity for humans coexisting with large carnivores. *Journal of Human Evolution* 36, 275–282.
- Treves, A., Plumptre, A.J., Hunter, L.T.B., Ziwa, J., 2009. Identifying a potential lion *Panthera leo* stronghold in Queen Elizabeth National Park, Uganda, and Parc National des Virunga, Democratic Republic of Congo. *Oryx* 43, 60–66.
- Uganda Wildlife Authority, 2000. *Queen Elizabeth National Park, Kyambura Wildlife Reserve, Kigezi Wildlife Reserve General Management Plan*. Uganda Wildlife Authority, Kampala, Uganda.
- Vickery, W.L., Giraldeau, L., Templeton, J.J., Kramer, D.L., Chapman, C.A., 1991. Producers, scroungers, and group foraging. *American Naturalist* 137, 847–863.
- Waser, P.M., 1981. Sociality or territorial defense? The influence of resource renewal. *Behavioral Ecology and Sociobiology* 8, 231–237.
- Waser, P.M., 1987. Interactions among primate species. In: Smuts, D.L.C.B.B., Seyfarth, R.M., Wrangham, R.W., Struhsaker, T.T. (Eds.), *Primate Societies*. University of Chicago Press, Chicago, pp. 210–226.
- Waser, P.M., Wiley, R.H., 1979. Mechanisms and evolution of spacing in animals. In: Marler, J.G.V. P. (Ed.), *Handbook of Behavioral Neurobiology: Social Behavior, Communication*. Plenum Press, New York, pp. 159–215.
- Wegge, P., Pokheral, C.P., Jnawali, S.R., 2004. Effects of trapping effort and trap shyness on estimates of tiger abundance from camera trap studies. *Animal Conservation* 7, 251–256.
- Woodroffe, R., Ginsberg, J.R., 1998. Edge effects and the extinction of populations inside protected areas. *Science* 280, 2126–2128.
- Wrangham, R.W., Gittleman, J.L., Chapman, C.A., 1993. Constraints on group size in primates and carnivores: population density and day range as assays of exploitation competition. *Behavioral Ecology and Sociobiology* 32, 199–210.
- Zug, R., 2009. *Individual Identification and Habitat Use of Andean Bears on Private Lands in the Ecuadorian Andes*. In: Nelson Institute for Environmental Studies, University of Wisconsin-Madison, Madison, WI.