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Factors Influencing Ranging on Community Land and Crop Raiding by Mountain Gorillas

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human–wildlife conflict; crop raiding; mountain gorillas; wildlife conservation; food availability; conflict mitigation; land-use strategy; ecological factors.

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Abstract

One of the challenges facing conservationists is the conflict between humans and wildlife due to competition for resources. Ranging outside the national park and crop raiding by mountain gorillas *Gorilla beringei beringei* around Bwindi Impenetrable National Park, Uganda, is a major concern because it has negative impacts on both wildlife conservation and local livelihoods, particularly due to the high density of subsistence agriculturalists living along the park boundary. The objective of this study was to investigate the effects of food availability inside and outside the park on the occurrence of gorillas ranging outside the park and crop raiding. We collected data on 13 mountain gorilla groups ranging in three general locations on the edge of the park over a 13-month period. Using generalized linear mixed models, we found that the number of days both ranging outside the park and crop raiding was positively influenced by the availability of both tea *Camellia sinensis* and pine (*Pinus* sp.) plantations and uncultivated land, all of which contain herbaceous plants eaten by the gorillas, as well as due to the availability of palatable crops [bananas (*Musa* sp.), eucalyptus (*Eucalyptus* sp.) and sweet potatoes *Ipomoea batatas*]. Our results suggest that ranging outside the park and crop raiding were influenced by food availability outside the park, not by a lack of food resources inside the park. To stop gorillas from leaving the park, we recommend removing herbaceous foods consumed by gorillas from plantations and uncultivated land and planting of buffer crops. If kept clear of herbaceous foods and planted contiguously along the boundary, tea plantations may best serve as a buffer to prevent gorillas from using community land. This study shows that the mitigation of human–wildlife conflict requires research to inform appropriate management strategies based on the species' behavioral ecology.

Introduction

A major challenge facing wildlife conservation is the conflict arising from the increasing interaction between humans and wildlife (Woodroffe, Thirgood & Rabinowitz, 2005). This conflict is neither new nor rare, but through extensive transformation of natural habitats an increasing number of wildlife species are forced into close proximity with humans, thereby intensifying this conflict (Woodroffe *et al*., 2005; Sih, Ferrari & Harris, 2011). Large mammals can cause high economic losses through preying upon livestock (Treves & Karanth, 2003) or consuming cultivated crops (Sukumar, 1990), can generate anxiety or disempowerment (Madden, 2008) and can even cause human injury and death (Packer *et al*., 2005). Human–wildlife conflict generates negative attitudes by local communities toward wildlife, thereby compromising biodiversity conservation efforts (Hill, 2000; Linkie *et al*., 2007; Dickman, 2010). To mitigate such conflict, factors influencing the occurrence of crop raiding should be examined.

Wildlife ranging outside protected areas and crop raiding have been linked to many factors, including habitat quality, availability of food resources inside a protected area, proximity to cultivated food, patterns of cultivation, levels of human activity, types of barriers between forest and farmland, availability and distribution of water and potential risks associated with raiding (Nyhus, Tilson & Sumianto, 2000; Sitati *et al*., 2003; Osborn, 2004; Sitati, Walpole & Leader-Williams, 2005; Linkie *et al*., 2007; Jackson *et al*., 2008; Hockings, Anderson & Matsuzawa, 2009). Furthermore, the frequency of raiding increases with availability of crops, which are often energy-rich, spatially clumped and offer increased foraging efficiency compared with natural foods (Sukumar, 1990; Naughton-Treves *et al*., 1998). This positive relationship was seen in chimpanzees *Pan troglodytes* and orangutans *Pongo* sp. (Hockings & Humle, 2009; Hockings *et al*., 2009; Campbell-Smith *et al*., 2011; Hockings & McLennan, 2012). However, chimpanzees appear to crop raid more frequently during times of wild fruit scarcity (Naughton-Treves *et al*., 1998; Hockings &

Humle, 2009; Hockings *et al*., 2009; McLennan, 2013). There are some reports on crop raiding by bonobos *Pan paniscus* and western gorillas *Gorilla gorilla*; however, nothing is known about the ecological correlates causing this behavior (Hockings & Humle, 2009). Across Africa, great apes increasingly range within human-modified landscapes. This direct contact gives rise to competition and conflict between apes and humans (Campbell-Smith *et al*., 2011; McLennan & Hockings, 2014).

Critically endangered mountain gorillas (hereafter gorillas) in Bwindi Impenetrable National Park (hereafter Bwindi) and the Virunga Conservation Area sometimes range outside the protected areas and raid cultivars (Goldsmith, Glick & Ngabirano, 2006; Hockings & Humle, 2009). Crop raiding negatively affects subsistence of local communities and this often results in harassment or displacement of wildlife or retaliation killing (Woodroffe *et al*., 2005). Even if not crop raiding, gorillas ranging outside a protected area might present a risk for human safety, especially in areas with a high human population density (Goldsmith *et al*., 2006). For local people, gorillas can be a source of economic devastation, anxiety, injury and personal danger (Madden, 2006, 2008). Gorillas face a higher potential of disease transmission from humans and livestock, uncontrolled contact with humans and waste, and harassment by local people (Nizeyi *et al*., 2002; Rwego *et al*., 2008; Nkurunungi & Ampumuza, 2014; N. Seiler, pers. obs.). In Bwindi, baboons *Papio anubis* and bushpigs *Potamochoerus larvatus* are more commonly encountered outside the park and cause more crop damage than gorillas (Olupot, Barigyira & Chapman, 2009; Akampulira, Bitariho & Mugerwa, 2015). However, large charismatic species, such as great apes, draw a great amount of attention due to their conservation value, size and the damage they may cause (Campbell-Smith, Sembiring & Linkie, 2012; Hockings & McLennan, 2012). Human–gorilla conflict is one of the major concerns for conservation managers in Bwindi (Uganda Wildlife Authority, 2014) and despite efforts to quantify the occurrences of it (e.g. Kalpers *et al*., 2010), few attempts have been made to understand its ecological causes. Additionally, the density of gorillas in Bwindi is probably increasing (Roy *et al*., 2014); hence, it can be expected that the extent of human–gorilla conflict will intensify. The goal of this study was to understand factors influencing ranging outside the protected area and crop raiding by Bwindi gorillas to guide evidence-based conservation strategies.

The area surrounding Bwindi contains one of the highest rural population densities worldwide (200–360 people per km^2; Ministry of Planning and Economic Development, 1997). Cultivated fields of food crops, plantations of pine, eucalyptus and tea as well as uncultivated land occur along the sharp boundary between the national park and the bordering community land. Some land is not managed or purposely kept as close to natural forest as possible (e.g. at tourist accommodations) and contains the same herbaceous vegetation as in the adjacent forest (Hockings & Humle, 2009; N. Seiler, pers. obs.). Gorilla groups habituated to human presence vary in the frequency of time spent outside the park and crop raiding (Kalpers *et al*., 2010). In particular, one group (Nkuringo) spends more time outside than inside the park. In 2005 a buffer zone was established to counteract this group's ranging outside the park (Goldsmith *et al*., 2006), but it has not been managed, allowing for herbaceous vegetation and fruit trees to regenerate, creating excellent habitat for gorillas (Kalpers *et al*., 2010; N. Seiler, pers. obs.; see Supporting Information).

To reduce the frequency of gorillas ranging outside the park and crop raiding, it is necessary to relate these patterns to the availability of resources outside and inside the protected area, both of which vary over time and space (Ganas, Nkurunungi & Robbins, 2009; Seiler, unpubl. data). We predicted the number of days that gorillas range outside Bwindi and crop raid would increase with (1) decreasing fruit availability inside Bwindi; (2) decreasing herbaceous biomass inside Bwindi; (3) increasing availability of palatable crops outside Bwindi; (4) increasing availability of uncultivated land and pine plantations containing herbaceous plants outside Bwindi; (5) decreasing availability of unpalatable food (tea) outside Bwindi.

Materials and methods

Study site

The study was conducted in Bwindi Impenetrable National Park, Uganda (0°53′–1°08′N; 29°35′–29°50′E), between June 2012 and July 2013. Bwindi is an afromontane rainforest characterized by steep-sided hills, peaks and narrow valleys, 331 km^2 in size and between 1160 and 2607 m in altitude (McNeilage *et al*., 2001). Bwindi contains *c*. 400 gorillas in about 39 social groups (Roy *et al*., 2014), including 13 groups habituated for research and tourism located in three general locations on the edge of the park (Fig. 1).

Ranging and crop raiding data collection

To determine the number of days spent outside the park, we recorded the location for 13 habituated gorilla groups by walking along the gorillas' trails or following the group (see Supporting Information). We recorded tracklogs using a Garmin global positioning system (GPS) (GPSmap 60CSx and 62) at 30-s intervals [$n = 141$ months of data cumulatively for all groups combined; 3–13 months per group; average sample days per month = 16 (range 2–31)]. The number of observation days per group varies mainly because some groups fissioned off from others and one group disintegrated during the study period.

We plotted the GPS data in ArcGIS 9.3 (ESRI Inc., Redlands CA, USA). We assigned location points for each day as inside or outside Bwindi to determine the number of days the gorillas left the park. We assigned the days gorilla ranged both inside and outside as being outside the park, independent on the amount of time they spent inside or outside the park on a respective day. We included all GPS

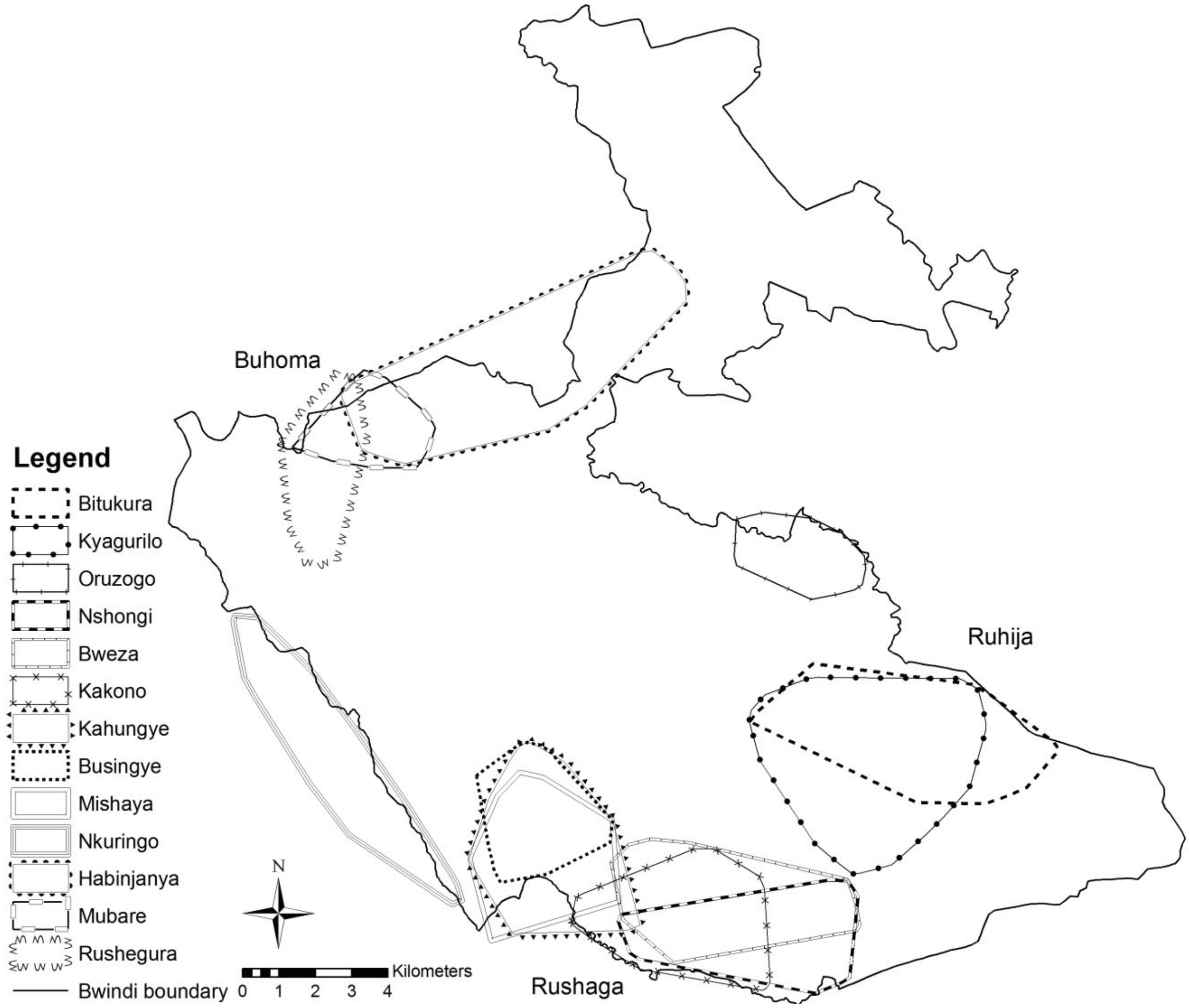

Figure 1 Map of Bwindi Impenetrable National Park and the three general locations where the habituated gorilla groups range (Buhoma, Rushaga and Ruhija). The home ranges are 100% minimum convex polygons and include all collected global positioning system locations. The names in the legend attached to a unique line style indicate the 13 study groups.

location points to determine 100% home ranges applying the minimum convex polygon method using Hawth's Tool for ArcGIS (Beyer, 2004) (Fig. 1).

A crop raiding incident was defined as a successful foray by a group to obtain cultivated food outside Bwindi, indicated by direct observations and/or feeding remains (Naughton-Treves *et al*., 1998; Hockings & Humle, 2009; Hockings *et al*., 2009). We noted what cultivars were consumed.

Food availability

To determine the spatial distribution of herb availability, we estimated the biomass of the most important food species (≥1% occurrence in diet per group in any given month). Biomass was determined using 490 transects of 200-m length, each randomly placed within a 500 × 500 m grid overlaid onto a map including the home ranges. Ten nested quadrats on alternate sides along each transect in intervals of 20 m were sampled. For herbs, we measured stem length and counted leaves in 1 m^2 plots, shrubs were counted in 5 m^2 and trees were sampled in 10 m^2 plots by measuring diameter at breast height (for more details, see Ganas *et al*., 2009).

We estimated the biomass of herbs using regression equations relating to the respective measure (number of leaves or stem length) recorded in the vegetation sampling to the dry weight of sampled individuals. We used regression equations from Ganas *et al*. (2009) and Seiler (unpubl. data). We calculated an average herb biomass g m^{-2} per group using only the transects included in a group's home range. Because of the low temporal variability of herb biomass in

Table 1 Percent availability of crop categories for all study groups

Season	Group	Palatable crops	Other crops	Uncultivated land	Pine plantations	Tea plantations
Dry	Bitukura	21.63	7.23	10.36	29.23	4.85
Wet	Bitukura	16.98	5.06	27.19	31.04	4.53
Dry	Busingye	6.66	16.91	73.57	0.00	0.00
Wet	Busingye	7.06	20.41	36.31	0.00	0.00
Dry	Bweza	23.11	12.46	44.27	0.00	0.00
Wet	Bweza	12.78	7.08	42.55	0.00	0.00
Dry	Habinjanya	2.54	6.07	67.75	9.65	11.56
Wet	Habinjanya	4.68	1.83	54.05	14.17	18.58
Dry	Kahungye	5.05	15.45	70.09	8.40	0.00
Wet	Kahungye	10.52	14.22	52.83	9.44	0.00
Dry	Kakono	13.23	13.45	54.80	8.38	0.00
Wet	Kakono	22.51	11.44	46.78	7.04	0.00
Dry	Kyagurilo	18.87	7.40	16.40	21.76	6.64
Wet	Kyagurilo	24.86	2.56	26.52	19.34	9.01
Dry	Mishaya	7.64	15.22	71.93	2.47	0.00
Wet	Mishaya	12.04	12.20	60.14	2.81	0.00
Dry	Mubare	6.62	4.70	77.55	1.14	8.20
Wet	Mubare	8.19	0.00	81.55	1.49	5.47
Dry	Nkuringo	0.00	5.50	94.50	0.00	0.00
Wet	Nkuringo	0.00	0.00	90.98	0.00	0.00
Dry	Nshongi	12.81	11.13	60.19	5.54	0.00
Wet	Oruzogo	9.22	2.44	4.39	39.86	43.54
Dry	Rushegura	8.22	5.41	75.43	1.12	8.06
Wet	Rushegura	10.61	1.71	76.31	1.65	6.06

Season indicates when the transects were walked and which time period they represent in the model. Dry season transects were walked in July and August 2012, representing June 2012–November 2012; wet season transects were walked in February and March 2013, representing December 2012–June 2013.

Bwindi (Ganas *et al*., 2009), we used one estimate per group for the whole study period.

To determine fruit availability, we monitored a total of 799 trees every month from 46 species known to provide fruits consumed by gorillas, noting the presence of ripe fruit (Goldsmith, 1999; see Supporting Information). Then we calculated a monthly fruit availability index using the formula:

$$A_m = \sum_{k=1}^{n} D_k B_k P_{km}$$

where D_k is the density of species k per km^2, B_k is the mean basal diameter of species k, P_{km} is the percentage of trees of species k showing ripe fruits in a month m and n is the total number of fruit species (Nkurunungi *et al*., 2004; Head *et al*., 2011). We calculated the fruit availability index for each group considering only the fruits consumed by that group based on direct observations and fecal analysis (Seiler unpubl. data).

To quantify the spatial distribution of cultivated foods outside Bwindi, we walked one transect in each general location around the park at a distance of 50 m parallel to the boundary (Fig. S3 found in Appendix S3) and recorded all land-use practices encountered (see Supporting Information). We walked transects twice to account for seasonal changes in crop availability (Table 1; see Supporting Information). Per transect we determined the length of the encountered land-use types in ArcGIS and pooled them in categories: tea plantations, uncultivated land including pine plantations, palatable crops (eucalyptus, bananas and sweet potatoes) and other crops not consumed by the gorillas. We then calculated the availability of each category for each gorilla group as percent distance of the total distance of the transect bordering the respective range of a group to get a comparable estimate of crop availability for all groups. We incorporated both seasonal measures of crop availability into the model.

Data analysis

To test our predictions, we developed two generalized linear mixed models (GLMMs; Baayen, 2008). The first model examined the influence of food availability both inside (herb biomass and fruit availability) and outside (availability of tea, uncultivated land and palatable crops) the park on the number of days per month gorillas ranged outside Bwindi. The second model investigated how the same factors influenced the number of days the gorillas crop raided.

For both models, we used a GLMM with Poisson error structure and log link function (McCullagh & Nelder, 1989).

We checked for a possible influence of within-group variation on the ranging outside and crop raiding patterns (see Supporting Information). To control for variation in the number of sample days per month and group, we included the number of observation days per group per month (log-transformed) as an offset term into the model. Aside from the fixed effects, we included group ID as a random effect to control for repeated observations on the same groups and the random slope of fruit availability within group ID to keep error I rate at the nominal level of 5% (Schielzeth & Forstmeier, 2009; Barr *et al.*, 2013). Additionally, for the first model, we included observation ID (i.e. a unique ID for each data point) as a random effect to account for overdispersion of the original model (dispersion parameter: 2.12). We log and square root transformed availability of tea and fruit, respectively. The other predictors were approximately symmetrically distributed. Additionally, we z-transformed all fixed effects to a mean of zero and a standard deviation of one to remove the influence of different units of our predictors (Schielzeth, 2010). As an overall test of the effects of the predictors, we compared the full model with a null model lacking all the fixed effects but comprising the same random effects and offset term as the full model (Forstmeier & Schielzeth, 2011) using a likelihood ratio test (Dobson, 2002). We assessed model stability by comparing the estimates derived by a model based on all data with those obtained from models with the levels of the random effect excluded one at a time, which revealed no problems for the first model. The second model was stable with regard to most predictors, except for considerable uncertainty for the effect of availability of palatable crops. Overdispersion was not an issue (dispersion parameter first model/second model = 0.3/0.7). To assess collinearity we determined variance inflation factors (Field, 2005) using the function vif of the R package car (Fox & Weisberg, 2011) applied to a standard linear model lacking the random effects and offset term. Collinearity was not an issue (see Supporting Information). The significance of each individual predictor variable was based on likelihood ratio tests comparing the full models with respective reduced models (Barr *et al.*, 2013). The total sample size was 141 observations of 13 groups across up to 13 months. The models were implemented in R (R Core Team, 2014) using the function glmer of the package lme4 (Bates *et al.*, 2014).

Because of instability issues regarding availability of palatable crops in the second model, we checked the coefficients of the stability test and identified two gorilla groups, which, when excluded, resulted in very different values: when we excluded Rushegura and Nkuringo group, the model revealed a very low and an extremely high estimate, respectively. Hence, we excluded these two groups (one at a time), ran the same full model again and compared the results for the individual predictors with those obtained from all data. Collinearity and overdispersion were not an issue. Model stability was good, except for the effect of herbaceous biomass. To be consistent in the analysis, we also excluded these two groups from the first model. Collinearity and overdispersion were not an issue.

Results

Ranging outside the park

Eleven out of 13 gorilla groups spent 2–98% of the observation days outside the park (Fig. 2).

There was a clear impact of the predictors on the number of days gorillas ranged outside the park [likelihood ratio test: $\chi^2 = 16.418$, degrees of freedom (d.f.) = 5, $P = 0.006$]. More specifically, the number of days gorilla groups ranged outside the park increased with increasing availability of both uncultivated land and tea outside the park (Table 2; Fig. 3a,b). Palatable crops outside the park and food availability inside the park (herbaceous vegetation and fruit) were not significantly related to days spent outside the park.

We reran the model while excluding each of the two groups causing uncertainty regarding the availability of palatable crops in the second model. The model results did not change when we removed Rushegura group and the same predictors were significant. When we excluded Nkuringo group from the model, the test predictors had a clear overall effect on the response ($\chi^2 = 29.283$, d.f. = 5, $P < 0.001$), with the days gorilla groups spent outside the park being positively correlated with all three variables measuring food availability outside the park (uncultivated land, tea and palatable crops) but not with food availability inside the park (Table 3).

Crop raiding

Only five out of 13 groups were observed to crop raid (Fig. 4), including groups in all three locations throughout

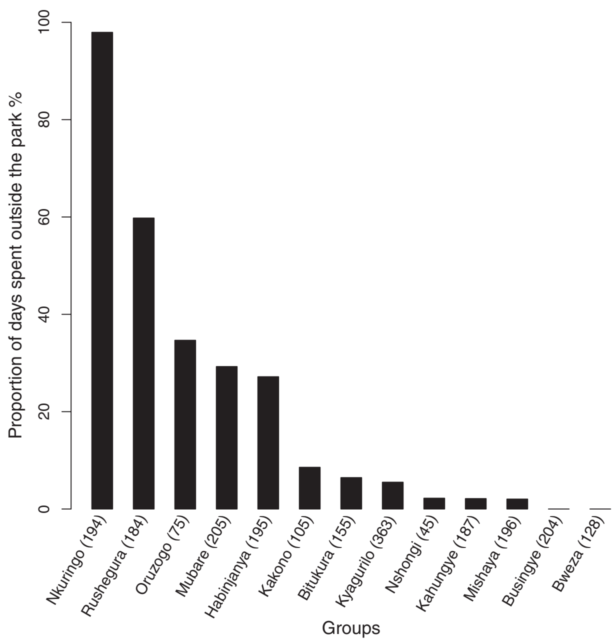

Figure 2 Proportion of days spent outside the national park per group with number of total observation days per group in parentheses.

Table 2 Summary of GLMM explaining the number of days gorillas ranged outside Bwindi

Term	Estimate	SE	χ^2	*P*-value	Min[a]	Max[a]
Intercept	−3.179	0.318	[b]	[b]	−3.717	−2.971
Fruit availability	−0.234	0.145	2.866	0.090	−0.597	−0.144
Herbaceous biomass inside the park	−0.073	0.306	0.057	0.812	−0.303	0.287
Availability of palatable crops	0.376	0.378	1.014	0.314	0.119	0.669
Availability of tea	1.123	0.288	11.641	0.001	0.950	1.494
Availability of uncultivated land and pine plantations	1.495	0.467	9.570	0.002	1.299	1.909

[a]Minimum and maximum of the estimates derived from datasets excluding the levels of the random effects one at a time.
[b]Not shown because of having no meaningful interpretation.
GLMM, generalized linear mixed models; SE, standard error.

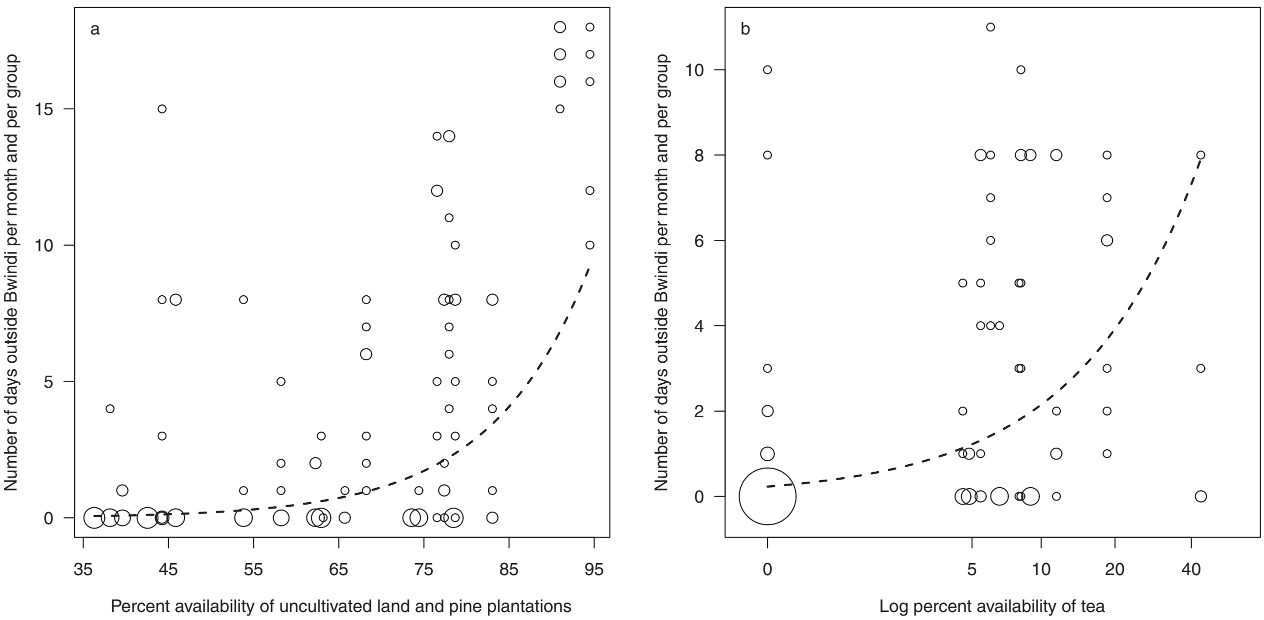

Figure 3 (a) Influence of availability of uncultivated land and pine plantations on the amount of days each gorilla group spent outside the national park per month [estimate + standard error (SE) = 1.495 ± 0.467, χ^2 = 9.570, P = 0.002]. The area of the circles indicates the number of observations (n = 141), and the dashed line indicates the fitted influence of availability of uncultivated land and pine plantations on the number of days each gorilla group spent outside the national park per month, with all other predictor variables in the model being at their average. (b) Influence of availability of tea on the amount of days each gorilla group spent outside the national park per month (estimate + SE = 1.123 ± 0.288, χ^2 = 11.641, P = 0.001). The area of the circles indicates the number of observations (n = 141), and the dashed line indicates the fitted influence of availability of tea on the number of days each gorilla group spent outside the national park per month, with all other predictor variables in the model being at their average.

Table 3 Summary of GLMM explaining the number of days gorillas ranged outside Bwindi after excluding Nkuringo group (see Supporting Information for explanation)

Term	Estimate	SE	χ^2	*P*-value	Min[a]	Max[a]
Intercept	−3.717	0.289	[b]	[b]	−3.957	−3.478
Fruit availability	−0.245	0.174	2.030	0.154	−0.400	−0.148
Herbaceous biomass inside the park	0.287	0.259	1.192	0.275	0.082	0.447
Availability of palatable crops	0.669	0.308	4.596	0.032	0.441	1.092
Availability of tea	1.494	0.235	25.536	<0.001	1.388	1.633
Availability of uncultivated land and pine plantations	1.395	0.414	11.802	0.001	1.051	1.750

[a]Minimum and maximum of the estimates derived from datasets excluding the levels of the random effects one at a time.
[b]Not shown because of having no meaningful interpretation.
GLMM, generalized linear mixed models; SE, standard error.

Table 4 Proportions of raided crops per group

Crop	Part eaten	Nkuringo group	Rushegura group	Mubare group	Habinjanya group	Oruzogo group
Banana (*Musa* sp.)	Pith	58.1% (43)	52% (26)	–	25% (1)	–
Eucalyptus (*Eucalyptus* sp.)	Bark	13.5% (10)	48% (24)	100% (15)	75% (3)	–
Sweet potato *Ipomoea batatas*	Leaves	17.6% (13)	–	–	–	–
Maize *Zea mays*	Pith	5.4% (4)	–	–	–	–
Passion fruit *Passiflora edulis*	Fruit	5.4%(4)	–	–	–	–
Coffee (*Coffea* sp.)	Fruit	–	–	–	–	100% (3)

Numbers in % indicate the proportion that each crop contributed to all crop raiding events for each group, and the numbers in parentheses represent the number of feeding incidences per food item per group obtained through direct observations and/or feeding remains.

Table 5 Summary of GLMM explaining the number of days the gorillas raided crops

Term	Estimate	SE	χ^2	*P*-value	Min[a]	Max[a]
Intercept	–6.260	0.866	[b]	[b]	–25.564	–5.938
Fruit availability	–0.015	0.114	0.017	0.896	–0.124	0.041
Herbaceous biomass inside the park	–0.932	0.833	1.019	0.313	–2.000	–0.779
Availability of palatable crops[c]	0.294	0.550	0.286	0.593	–1.174	8.835
Availability of tea	1.821	0.618	8.381	0.004	1.520	17.602
Availability of uncultivated land and pine plantations	3.356	1.002	15.153	<0.001	2.367	15.725

[a]Minimum and maximum of the estimates derived from datasets excluding the levels of the random effects one at a time.
[b]Not shown because of having no meaningful interpretation.
[c]Uncertainty about the impact of this predictor due to model instability issues.
GLMM, generalized linear mixed models; SE, standard error.

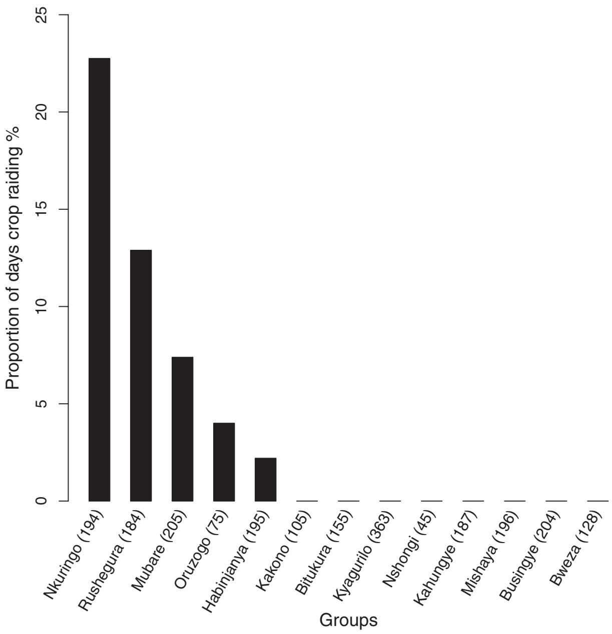

Figure 4 Proportion of days crop raiding occurred per group with number of total observation days per group in parentheses.

the park. Banana pith and eucalyptus bark were the most often raided crops (Table 4).

There was a clear impact of the fixed effects on the number of days gorillas crop raided ($\chi^2 = 15.38$, d.f. = 5, $P = 0.009$). More specifically, there was a positive relationship between number of days crop raiding and availability of uncultivated land and tea (Table 5; Fig. 5a,b). The impact of the availability of palatable crops, although not significant, cannot be ascertained as we had model instability issues with this predictor. Furthermore, there was no influence of the availability of food inside the park on days crop raiding.

When we removed Rushegura group from the model, the results were essentially the same as for the original full model. After dropping Nkuringo group, the full model was still significantly different from the null model ($\chi^2 = 23.09$, d.f. = 5, $P < 0.001$), but palatable crops positively influenced crop raiding in addition to the same predictors as for the original full model. The effect of herbaceous biomass inside the park on the number of days groups crop raided was uncertain due to model instability issues; however, fruit availability did not have any significant impact (Table 6).

Discussion

In anthropogenic-influenced habitats, wildlife often occurs in isolated remnants of suitable habitat. Large mammals, such as elephants or large carnivores, may come into conflict with humans as they move through such landscape mosaics (Woodroffe *et al.*, 2005; Wilson *et al.*, 2013). Patterns of crop raiding and carnivore depredations are often species specific and hence mitigations strategies should be as well. However, important generalizations can only be made by examining species' conflict patterns and understanding the underlying patterns and processes (Sitati *et al.*, 2003; Jackson *et al.*, 2008).

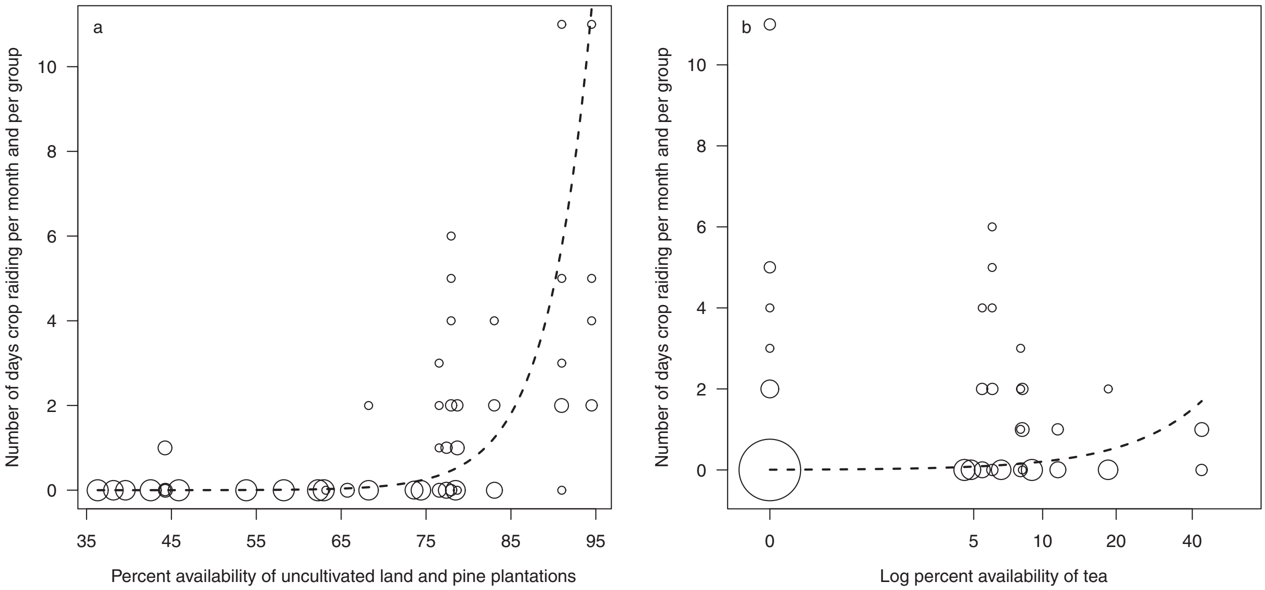

Figure 5 (a) Influence of availability of uncultivated land and pine plantations on the amount of days each gorilla group was crop raiding per month [estimate + standard error (SE) = 3.356 ± 1.002, χ^2 = 15.153, P < 0.001]. The area of the circles indicates the number of observations (n = 141), and the dashed line indicates the fitted influence of availability of uncultivated land and pine plantations on the number of days each gorilla group raided crops per month, with all other predictor variables in the model being at their average. (b) Influence of availability of tea on the amount of days each gorilla group was raiding crops per month (estimate + SE = 1.821 ± 0.618, χ^2 = 8.381, P = 0.004). The area of the circles indicates the number of observations (n = 141), and the dashed line indicates the fitted influence of availability of tea on the number of days each gorilla group raided crops per month, with all other predictor variables in the model being at their average.

Table 6 Summary of GLMM explaining the number of days gorillas raided crops after excluding Nkuringo group (see Supporting Information for explanation)

Term	Estimate	SE	χ^2	P-value	Min[a]	Max[a]
Intercept	–25.564	6.784	[b]	[b]	–98.158	–9.929
Fruit availability	–0.026	0.117	0.050	0.823	0.242	0.063
Herbaceous biomass inside the park[c]	–1.464	0.763	3.100	0.078	–9.023	0.354
Availability of palatable crops	8.836	2.672	11.169	0.001	1.734	35.696
Availability of tea	17.602	5.407	20.386	<0.001	4.871	75.952
Availability of uncultivated land and pine plantations	15.725	4.198	18.644	<0.001	3.689	56.459

[a]Minimum and maximum of the estimates derived from datasets excluding the levels of the random effects one at a time.
[b]Not shown because of having no meaningful interpretation.
[c]Uncertainty about the impact of this predictor due to model instability issues.
GLMM, generalized linear mixed models; SE, standard error.

Although relationships between food availability and conflict patterns of other large mammals, such as elephants (Sukumar, 1990; Hoare, 1999; Gubbi, 2012) and large carnivores (Kolowski & Holekamp, 2006; Sangay & Vernes, 2008; Inskip & Zimmermann, 2009), have received a lot of research attention, this is the first study to examine how food availability both within and outside a protected area influences how much gorillas range outside the park and crop raid. The more uncultivated land, pine and tea plantations, and palatable crops available, the more the gorillas ranged outside Bwindi and raided crops. Against our predictions, the availability of food resources inside the park had no influence on the number of days groups ranged outside the park or crop raided. Hence, there appears to be no need for gorillas to supplement their diet with crops in times of low fruit availability as abundant and high-quality herbaceous vegetation is available throughout the year (Nkurunungi *et al*., 2004; Ganas *et al*., 2009). In sum, what was available along the park boundary was driving gorilla foraging outside the park and crop raiding, not a lack of food resources within the forest. This is in contrast to chimpanzees, who are mainly frugivorous and increased crop raiding during times of forest fruit scarcity (Hockings & Humle, 2009; Hockings *et al*., 2009; McLennan, 2013). Understanding the relationship between crop raiding or depredation patterns and human land-use practices is crucial in designing effective management strategies to reduce human–wildlife conflict (Seidensticker, 1984; Naughton-Treves *et al*., 1998). Although our research focused on one species and the parameters of this study may be rather specific, as is typically the case for such studies, the findings are applicable and the methodology is transferable to other sites and species.

Besides food availability, several factors may play a role in ranging and crop raiding patterns (e.g. Linkie *et al*., 2007; Jackson *et al*., 2008). For gorillas, the loss of fear of humans by habituated gorillas may have worsened the situation, although they raided cultivated foods before habituation began (Madden, 2006). We recorded one newly habituated group (Oruzogo) crop raiding, whereas one group (Kyagurilo) that has been habituated since the early 1990s has never been recorded to crop raid (Kalpers *et al*., 2010; this study). Additionally, unhabituated groups have raided crops outside the national park (P. Ezuma, pers. comm.). Although habituation may increase the likelihood of crop raiding, most raiding wildlife is initially unhabituated to human presence. However, conflict may still occur as animals may adjust their behavior to avoid humans (Wilson, Hauser & Wrangham, 2007; Valeix *et al*., 2012) or lose their fear of humans (Sitati *et al*., 2005).

Influence of availability of uncultivated land, pine and tea plantations

Land-use practices in areas bordering national parks have been shown to play a major role in human–wildlife conflict with several primate species (Naughton-Treves *et al*., 1998; Saj *et al*., 2001; Yihune, Bekele & Tefera, 2009), large carnivores (Palmeira *et al*., 2008; Sangay & Vernes, 2008; Zarco-González, Monroy-Vilchis & Alaníz, 2013) and elephants (Chiyo *et al*., 2005; Wilson *et al*., 2013). For example, Nyhus *et al*. (2000) reported a positive relation between the presence of forest cover adjacent to agricultural areas and elephant crop raiding. Our study also shows the impact of land-use practices as we found a positive relation between uncultivated land and pine plantations available and the number of days gorillas ranged outside Bwindi and crop raided. Uncultivated land has been left unmanaged and contains herbaceous plants and fruit trees regularly consumed by the gorillas. Against our prediction, tea, which is often used as a buffer crop (Rode *et al*., 2006), did not work as a deterrent against gorillas ranging outside the park and crop raiding. Gorillas did not feed on tea or pine trees but consumed the herbaceous vegetation growing in between (Hockings & Humle, 2009; N. Seiler, pers. obs.). Additionally, tea plantations are interspersed with cultivated and uncultivated land and currently do not form a contiguous barrier to stop gorillas from ranging further into community land. Through poor management of land adjacent to the national park, the effect of a buffer crop can get inverted. In effect, the plantations and uncultivated land have turned into an extension of the intact forest, providing attractive habitat for gorillas.

Influence of availability of palatable crops

The availability of cultivated plants is a major factor influencing crop raiding of large mammals such as elephants (Sukumar, 1990; Nyhus *et al*., 2000; Sitati *et al*., 2003; Chiyo *et al*., 2005; Gubbi, 2012), chimpanzees (Naughton-Treves *et al*., 1998; Hockings & McLennan, 2012), orangutans (Campbell-Smith *et al*., 2011), olive baboons and red-tailed monkeys (Maples *et al*., 1976; Naughton-Treves *et al*., 1998), and wild boar *Sus scrofa* (Schley *et al*., 2008). In line with this and our prediction, after excluding Nkuringo group from the analysis (see Methods and Supporting Information for justification), there was a positive relationship between the number of days gorillas ranged outside the park and crop raided and the availability of palatable crops. Banana and eucalyptus were the most often raided crops in Bwindi. Banana pith is high in sugars (Ganas, unpubl. data) and eucalyptus bark is especially high in sodium (Rode *et al*., 2003), a scarce resource in the tropics and one of the most limiting nutrients of herbivores (McNaughton, 1988) and gorillas (Rothman, Van Soest & Pell, 2006). Our results conform to the widespread view that crops are raided for their high nutritional value as it has been suggested for elephants, chimpanzees and several monkey species (Sukumar, 1990; Naughton-Treves *et al*., 1998; Hockings & McLennan, 2012).

Management strategies to reduce human–gorilla conflict

Mitigation measures, such as crop guarding or pushing gorillas back into the park, appeared to work in the short term and had led to a significant reduction in cultivar losses due to gorillas (Aharikundira & Tweheyo, 2011). However, gorillas are adaptive and can change their behavior by visiting fields at night (Hockings & Humle, 2009). Such behavioral adaptations have also been reported for other species, for example, elephants (Gunn *et al*., 2014), lions *Panthera leo* (Valeix *et al*., 2012) and chimpanzees (Wilson *et al*., 2007; Krief *et al*., 2014). Hence, such mitigation measures treat the symptoms but do not target the underlying causes (Jackson *et al*., 2008).

Although mitigation strategies must be site specific, edge management around national parks seems to be a crucial aspect regardless of the species or site (Naughton-Treves *et al*., 1998; Saj *et al*., 2001; Chiyo *et al*., 2005; this study). Consequently, recommendations to alleviate human–wildlife conflict often involve implementing appropriate land-use strategies that deter wildlife in areas adjacent to protected areas (Palmeira *et al*., 2008; Sangay & Vernes, 2008; Nijman & Nekaris, 2010; Gubbi, 2012; Guerbois, Chapanda & Fritz, 2012; Zarco-González *et al*., 2013). Management strategies in Bwindi should focus on discouraging gorillas from leaving the park by converting land outside the park into unattractive feeding grounds. Gorillas prefer food rich in sugar and sodium but low in fiber (Rothman *et al*., 2006; Ganas, Ortmann & Robbins, 2008). Hence, we recommend planting unpalatable buffer crops that are high in fiber and secondary compounds such as tea, timber or sisal (Chiyo *et al*., 2005; Hockings & Humle, 2009). Plantation of crops, such as bananas or eucalyptus, should be avoided as they attract wildlife (Goldsmith *et al*., 2006; Rode *et al*., 2006; this study). Ideally, buffer crops should be unpalatable, planted over large areas and be economically valuable as it has been suggested for chilies to deter crop raiding elephants (Parker & Osborn, 2006; Webber *et al*., 2011). Tea plantations, if kept clear of any herbaceous vegetation and planted continuously along the boundary, could be a good alternative for Bwindi as they could also provide income for local people (Madden, 2004; Kalpers *et al*., 2010). Tea has proven to be a successful buffer crop against other raiding animals in the northern part of the park (Aharikundira & Tweheyo, 2011) and seems to work as a barrier for chimpanzees (Hockings & Humle, 2009). We recommend removing herbaceous foods and fruit trees growing on uncultivated land and in plantations of pine and tea, and subsequently maintain the land to keep it clear of gorilla food species. Our study stresses the need for data on what crops and which land-use strategies have the potential to cause or reduce human–wildlife conflict (Hockings & McLennan, 2012).

Conclusions

Human–wildlife conflicts may result in direct negative human–wildlife interactions as well as antagonisms between conservation and other human interests (Dickman, 2010; Peterson *et al*., 2010; Guerbois *et al*., 2012). Our results suggest that the actual extent of crop raiding by gorillas around Bwindi is relatively small. However, perceptions of farmers losing all their crops due to raiding large mammals, such as gorillas, can be very negative, as they are shaped by the extent of the loss as well as by numerous environmental, technological and social factors relating to individual vulnerability and risk (Naughton-Treves & Treves, 2005). Crop raiding, attacks on humans, the failure of park authorities to address human–wildlife conflicts adequately as well as a lack of empowerment contribute to undermining the benefits local people gain from wildlife, such as tourism, and instead increase hostility and anger toward the park and conservation efforts. Hence, local perceptions of damage and injury caused by wildlife, including gorillas, might not reflect an objective measure but represent the local communities' unmet expectations and perceived risks (Hill, 1997; Madden, 2004, 2008; Naughton-Treves & Treves, 2005; Tumusiime & Svarstad, 2011), leading to a human–human conflict about wildlife (Guerbois *et al*., 2012; Redpath, Bhatia & Young, 2015).

We have shown that it is important that conservation managers devote resources to understand the ecological causes of human–wildlife conflict, so as to find ways to mitigate and eventually prevent these conflicts. As shown here and elsewhere (Sukumar, 1990; Naughton-Treves *et al*., 1998; Chiyo *et al*., 2005), wildlife does not necessarily raid crops as an answer to forest food scarcity but is attracted by certain land-use types outside the protected area. Conservation efforts need to be taken beyond national park boundaries and failure to properly manage areas adjacent to protected areas may leave the conflict unaddressed or worsen it (Wikramanayake *et al*., 1998; Fernando *et al*., 2005; Madden, 2008). This study illustrates that the mitigation of such conflict is complex and needs innovative and interdisciplinary approaches (Dickman, 2010; Redpath *et al*., 2015), integrating the underlying human dimension as well as research to inform appropriate management strategies based on the species' behavioral ecology. However, we acknowledge that changing land-use practices in favor of those that deter wildlife must consider the needs of wildlife while also being supported by local communities, policies and legal frameworks at the national level (Madden, 2008).

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Supporting information

Additional Supporting Information may be found in the online version of this article at the publisher's web-site:

Appendix S1. The Nkuringo group and buffer zone.
Appendix S2. Gorilla location data collection.
Appendix S3. Food availability.
Appendix S4. Collinearity control.
Appendix S5. Between-group versus within-group effects.