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The nutritional value of feeding on crops: Diets of vervet monkeys in a humanized landscape

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Abstract
Anthropogenic influences have dramatically altered the environments with which primates interact. In particular, the introduction of anthropogenic food sources to primate groups has implications for feeding behaviour, social behaviour, activity budgets, demography and life history. While the incorporation of anthropogenic foods can be beneficial to primates in a variety of nutritional ways including increased energetic return, they also carry risks associated with proximity to humans, such as risk of being hunted, disease risk and risk of conflict. Given such risks, we initiated a 3-year study where we sought to understand the underlying nutritional motivations for anthropogenic food resource use by vervet monkeys (*Cercopithecus aethiops*) in the humanized matrix surrounding the Nabugabo Field Station in central Uganda. Feeding effort, defined as proportion of feeding scans spent on anthropogenic food, was not associated with ripe fruit availability nor with crop availability as determined by phenological monitoring. Likewise, there was no difference in the protein, fibre, or lipid composition of crop food items compared to wild food items. Individuals spent less time feeding overall in months over the 3 years with a higher proportion of time spent feeding on crop foods, suggesting a potential benefit in terms of accessibility (reduction in the proportion of activity budget devoted to feeding).

Résumé
Les influences humaines modifient considérablement les environnements dans lesquels vivent les primates. L'introduction de sources de nourriture d'origine humaine, particulièrement, a des implications pour le comportement alimentaire et social, pour la répartition des activités, la démographie et le cycle de vie. Si l'introduction de nourriture d'origine humaine peut être bénéfique de multiples façons pour les primates, notamment en matière de retour énergétique accru, elle peut aussi générer des risques liés à la proximité des hommes, comme la chasse, la maladie ou des conflits. Étant donné ces risques, nous avons lancé une étude de trois ans pour chercher à comprendre les motivations nutritionnelles sous-jacentes de l'utilisation des ressources alimentaires d'origine humaine par des grivets (*Cercopithecus aethiops*) dans la matrice humanisée qui entoure la station de terrain de Nabugabo, au centre de l'Ouganda. L'effort de recherche de nourriture, défini comme la proportion de recherche de nourriture passée sur des aliments d'origine humaine, n'était pas lié à la disponibilité de fruits mûrs ou de produits agricoles tel que défini par le

monitoring phénologique. De même, il n'y avait pas de différence dans la composition en protéines, fibres ou lipides des aliments provenant des cultures et ceux venant de la nature. Les individus ont passé moins de temps à se nourrir de produits des cultures, ce qui suggère un avantage potentiel en termes d'accessibilité (réduction de la part du budget d'activités consacrée à se nourrir).

KEYWORDS
anthropogenic, crop-raiding, human-modified landscapes, human–primate conflict, nutrition, nutritional geometry

1 | INTRODUCTION

Conversion of tropical rainforest to human-modified landscapes is one of the most prominent threats to biodiversity (Chapman & Peres, 2001; Estrada et al., 2017). Deforestation, estimated at 2.3 million km^2 between 2000 and 2012, is increasing at a rate of 2,101 km^2 per year in the tropics (Hansen et al., 2013). Models of deforestation have demonstrated that even had deforestation halted completely in 2010, the already established carbon emission and extinction debt would increase the extinction rate by 120% compared to 20th century extinction rates (Rosa, Smith, Wearn, Purves, & Ewers, 2016). Between 1999 and 2008, farmland in tropical countries expanded at an estimated rate of 48,000 km^2 annually, predominantly through the conversion of forest to crop or fallow field (Phalan et al., 2013).

As these anthropogenic pressures on primate habitat worsen, primate use of human-modified environments also becomes more common; wild primate groups are forced to alter their behavioural strategies in the light of these new ecological pressures. Increased reliance on human-modified landscapes can change ranging patterns (Koganezawa & Imaki, 1999; Sha & Hanya, 2013), demographic profiles (Singh & Rao, 2004), and increase group size (Biquand, Biquand-Guyot, Boug, & Gautier, 1992) as primate shift their land use and social behaviour. For example, edge-dwelling olive baboons that rely more heavily on crop foods have shorter interbirth intervals and lower infant mortality rates compared to forest-dwelling baboons who lack access to these crop resources (Higham et al., 2009). Similarly, in Indian langurs (*Semnopithicus ajax*; Borries, Sommer, & Srivastava, 1991), and capuchins (genus *Cebus*; Di Bitetti & Janson, 2001), anthropogenic food sources have been shown to increase the frequency of dominance interactions and lower infant mortality, respectively.

Despite our understanding of the relationship between enhanced food environments and primate ecology, little is known about the nutritional composition and characteristics of anthropogenic food items consumed by primates (McLennan & Ganzhorn, 2017; Riley, Tolbert, & Farida, 2013); however, such an understanding is needed to connect suggested behavioural effects of crop raiding to their underlying biological motivations. Among generalist, such as baboons and vervets, crop-raiding behaviours are adopted differently across individuals, age/sex categories, and groups (Strum, 2010), which may be related to differential nutritive needs, feeding skills, and risk payoffs. Thus, understanding the role of nutritional composition in motivating individuals to crop raid may offer new insights to predict and mitigate conflict (Hill, 2017; Riley et al., 2013; Strum, 2010). For example, as Tonkean macaques (*Macaca tonkeana*) target cacao (*Theobroma cacao*) that were higher in digestible carbohydrates than wild-growing fruits, Riley et al. (2013) suggested planting culturally, economically appropriate buffer crops that also is lower in carbohydrates would help mitigate some of the conflict that arises from primate crop raiding.

In this study, we seek to characterize the intensity, temporal pattern and nutritional implications of vervet monkey feeding on crop foods in a human-modified landscape in central Uganda. Vervet monkeys (*Cercopithecus aethiops*) are highly flexible generalist feeders (Kavanagh, 1978) known to thrive across a variety of landscapes and environments (Brennan, Else, & Altmann, 1985; Struhsaker, 1967). Vervets are more successful in degraded, fragmented or otherwise human-modified landscapes than any other African primate (Fisher & Owens, 2004; Lehman, 2004). In Uganda, primates (including vervet monkeys) are consistently identified as a top threat to crops, both in terms of frequency of raiding events and severity of crop losses (Hill, 1997; Hill, 2000; Naughton-Treves, 1998; Saj, Silcotte, & Paterson, 2001; Tweheyo, Hill, & Obua, 2005). Specifically, studies have documented that vervet crop raiding costs approximately $80–400 USD per farmer per season (Boulton, Horrocks, & Baulu, 1996; Saj et al., 2001).

The danger to primates in anthropogenic, crop dominated landscapes is illustrated at our study site Nabugabo Field Station in central Uganda (Chapman et al., 2016). Over 46-months vervet in this environment, seven of the group's 28 members were poisoned by bananas baited with herbicide with the intention of decreasing crop raiding, two members were captured by farmers for pets, and two individuals were killed by dogs that are often used to guard fields. This high potential for conflict with human populations creates a need to better understand primate crop raiding behaviours and resource-use patterns in human-modified landscapes, to effectively plan mitigation strategies permitted a more peaceful coexistence between humans and primates.

Beyond examining the nutritional composition of both wild and anthropogenic food items at Nabugabo, special consideration is made of the balance of nutrients in these food items. Nutritional geometry is an integrative framework for quantifying nutritional goals and intake in multi-dimensional, interactive space (Raubenheimer, Machovsky-Capuska, Chapman, & Rothman, 2015; Raubenheimer & Simpson, 1997). The framework quantifies complex nutritional environments by considering the dynamic, interactive nature of nutrients, as opposed to overemphasizing the role of any single nutrient (Felton, Felton, Lindenmayer, & Foley, 2009; Simpson & Raubenheimer, 1995).

At Nabugabo, we predict that crop foods will have nutritional benefits compared to wild food items, which may act as a motivator for the exploitation of anthropogenic foods. Typically, enhanced foods (including crop foods, garbage, and cooked/processed food products) are considered to offer a nutritional benefit to the individual by being nutrient dense (higher in energy per mass), higher in total nonstructural carbohydrates and fat, easily digestible (lower in fibre), and available in large, predictably spaced patches (i.e., crop fields and gardens) when compared to wild food diets (McLennan & Ganzhorn, 2017; Naughton-Treves, Treves, Chapman, & Wrangham, 1998; Nijman & Nekaris, 2010; Rode, Chiyo, Chapman, & Mcdowell, 2006). As a result, they offer a high reward, encouraging altered feeding strategies to incorporate anthropogenic food resources.

Second, we predict that a greater proportion of feeding efforts on crop feeding will reduce time spent feeding overall. A shift in primate feeding ecology to more anthropogenic diets has been shown to impact behaviour and life history. Wild diets supplemented with anthropogenic foods are associated with altered activity budgets (Forthman-Quick & Demment, 1988; Jaman & Huffman, 2013; Mckinney, 2011; Quick, 1986; Saj, Silcotte, & Paterson, 1999; Van Doorn, O'riain, & Swedell, 2010). For example, food supplementation led to decreases in proportion of time spent feeding and increases in proportion of time spent resting/inactive in baboons (*Papio anubis*; Altmann & Muruthi, 1988) and vervet monkeys (*Cercopithecus aeithiops*; Saj et al., 1999).

Lastly, we predict that crop feeding will increase when wild fruits are scarce and when crops are mature. Anthropogenic food resources can be especially important in times of wild food shortage and such food scarcity can be caused directly by anthropogenic disturbances, like deforestation (Freitas, Setz, Araújo, & Gobbi, 2008; Hill, 2000; Naughton-Treves et al., 1998; Tweheyo et al., 2005). For example, bearded capuchin monkeys (*Sapajus libidinosis*) in forest-farm mosaic environments exploited sugar cane and maize at a higher rate when forest fruit production was lowest in nearby forest fragments (Freitas et al., 2008). Likewise, Samango monkeys (*Cercopithecus albogularis labiatus*) in South Africa have been shown to increase their consumption of exotic plants during times when wild fruits are less available (Wimberger, Nowak, & Hill, 2017).

2 | METHODS

2.1 | Study site and subjects

This research was carried out along the shores of Lake Nabugabo, Uganda (8.2 × 5 km), which is a satellite of Lake Victoria that lies at an elevation of 1,136 m (0°22′–12°S and 31°54′E), and the Lake Nabugabo Research Station lies on the west side of the lake. The landscape around the research site comprises farmer's fields, degraded forest and a few buildings. The area receives an average of 1,348 mm of rain annually (Stampone, Hartter, Chapman, & Ryan, 2011). We followed a single habituated group (M group) over 3 years (June 2011 to May 2014). The group contained 22 individuals at the beginning of the study (two adult males, one subadult male, seven adult females, six subadult females, six juveniles and infants), but 30 individuals at the end (five adult males, eight adult females, three subadult females, 14 juveniles and infants).

2.2 | Behavioural observations

The group was followed 10 days a month, from June 2011 to May 2014 (36 months) and each day was approximately 9 hr (07:30 to 16:00). Scan samples of five group members were taken every 30 min. Two observers would move through the area occupied by all group members at the start of the half hour and locate animals in clear view to observe and their behaviour at first sighting was recorded. During these scans, we recorded the individual's identity, sex, age category, behaviour (e.g., resting, moving [including canopy/ground level], feeding [including detailed information on food species, part, height from ground while feeding, and feeding rate whenever possible], self-grooming, social behaviour [i.e., giving or receiving grooming, playing]), nearest neighbour (in metres). Ad libitum data were also collected on the group's interactions with people, dogs, cattle and crops (e.g., crop raiding, feeding).

2.3 | Phenological patterns of crop and wild food items

Monitoring food available began in June 2011, and involved quantifying the phenological state and average of multiple individuals of 24 tree and shrub species known to be consumed by the vervets (n = 67 individual trees/shrubs) (Table S1). If a tree on the phenology trail was removed (i.e., cut down), a new individual was added in the subsequent months as a replacement. Phenological data collected included ripe fruit, unripe fruit, flower, mature leaves and young leaves. Additionally, DBH was recorded monthly and used as an index of fruit production (as per Chapman et al., 1992).

Crop phenology was monitored within the group's home range from June 2011 to November 2013. The crops grown in the area are banana, maize, cassava, beans, Irish potatoes, sweet potatoes, guava and mango. Crop abundance was indexed as the number of metres of each vegetation type (e.g., fallow land, planted crops) along the forest edge, crop species present and its stage of ripeness.

2.4 | Nutritional analysis

All foods (both wild and anthropogenic) consumed by the vervet monkeys were collected as soon as possible after they were seen being eaten, and always within the week they were consumed. When possible, samples were taken from the same plant used by the individual, or from directly adjacent plants of the same species. Plants were processed identically to how vervets processed them for consumption. For example, if an individual only consumed the inner pulp of a fruit, only the inner pulp was used in nutritional analysis.

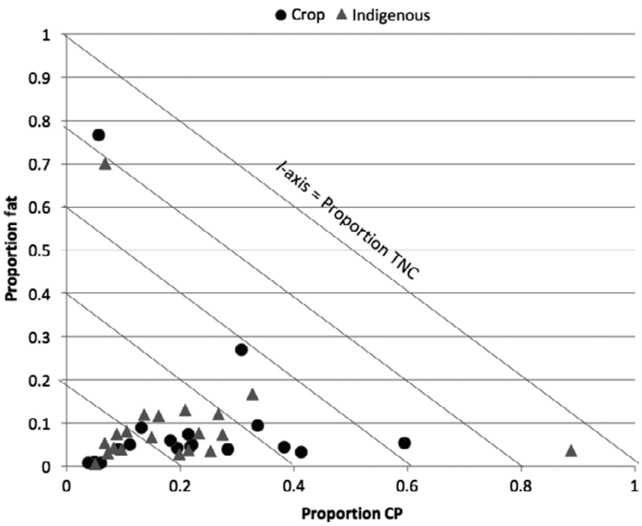

FIGURE 1 Right-angle mixture plot of nutritional values for crop food items and wild food items consumed by vervet monkeys at Nabugabo. TNC, total nonstructural carbohydrates; CP, crude protein

Samples were weighed and dried (away from direct sunlight at <40°C) immediately after collection, and milled in a 1-mm Wiley mill for transportation to Hunter College, New York (Rothman, Chapman, & Van Soest, 2012). Dried plant samples were analysed for their nutritional composition at Hunter College, New York, USA, in the department of Anthropology. Samples were analysed as per Rothman et al. (2012), for hemicellulose (via neutral detergent fibre), cellulose (via acid detergent fibre), lignin, total nonstructural carbohydrates (TNC), crude protein and fat. Fibre content was determined through neutral detergent fibre (NDF) and acid detergent fibre (ADF) using an A200 fibre analyzer (Macedon, New York). Samples were analysed for crude protein using the Leco TruSpec Nitrogen Analyzer (St. Joseph, Michigan), and multiplying the total nitrogen (N) by a factor of 6.25 (Rothman et al., 2012). Fat was measured via ether extract using an ANKOM XT15 Fat Analyzer (Macedon, New York). TNC was estimated by difference.

2.5 | Statistical analysis

Food items were grouped as wild or anthropogenic/crop foods. Nutritional composition was compared using nonparametric Mann–Whitney *U* tests, conducted in R statistical software. To test our predictions, general linear models were created to explore relationships between crop food feeding effort and (i) overall feeding effort, (ii) crop phenology and (iii) wild food availability/phenology. Temporal trends in crop food feeding effort were assessed using Box-Pierce tests of autocorrelation. Results are considered significant at $p = .05$.

3 | RESULTS

3.1 | Nutritional differences between crop and wild food items

Crop and wild foods differed in the relative proportions of nutrients they contained, with crop foods demonstrating higher proportions of nonstructural carbohydrates and proteins relative to fat, when compared to wild food items ($F = 2.95$, $p = .059$) (Figure 1). However, there were no significant differences in nutrient composition between crop and wild foods (TNC: $W = 565.5$, $p = .35$; Protein: $W = 894$, $p = .12$; Fat: $W = 657$, $p = .39$; Energy (kcal): $W = 678$, $p = .65$; Table 1).

3.2 | Effect of crop food use on activity budget and wild food feeding

As predicted, months with more feeding effort on crop foods had correspondingly lower feeding time on all foods relative to other activities ($R^2 = .14$, $p = .022$; Figure 2). Thus, crop food consumption is inversely related to feeding time.

3.3 | Dietary crop foods

Feeding behaviour accounted for a mean of 32.3% with a *SD* of ±7% of all scans. Of this total, an average of 14% ± 6% were on crop foods per month. This figure ranged from a low of 3% (June 2011) to a high of 25% of all monthly feeding scans (March, 2014) (Figure 3). In total, 90% of the vervet diet at Nabugabo based on foraging effort comprised of 53 foods, with the top 10 foods comprising 48% of the diet (Table 2). Sixteen of these 53 most commonly consumed foods were crop foods (Table 3). The most commonly exploited crop food was oil palm (*Elaeis guineesis*), which was the ninth most frequently consumed food.

TABLE 1 Average nutritional values and *SD* for crop foods and wild foods at Nabugabo, Uganda. All values are expressed as percent dry matter.

	NDF/DM	ADF/DM	ADL/DM	CP/DM	FAT/DM	TNC	ASH/DM	Energy (kCal)
Average crop/human food	36.7	27.3	10.9	13.6	5.5	43.1	5.2	270.8
SD	19.9	17.7	10.4	9.3	11.3	20.7	2.7	93.19
Average wild food	37.7	31.5	14.8	10.6	6.2	41.4	6.2	242.54
SD	14.3	13.8	8.6	9.1	10.3	18.7	2.5	99.80

NDF, neutral detergent fibre; ADF, acid detergent fibre; TNC, total nonstructural carbohydrates; CP, crude protein.

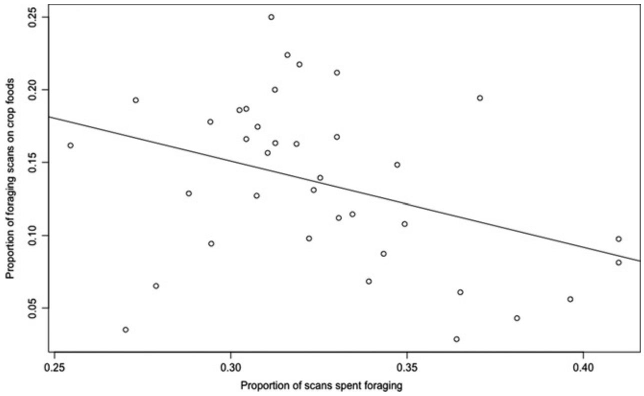

FIGURE 2 Relationship between overall feeding effort and feeding effort on crop foods

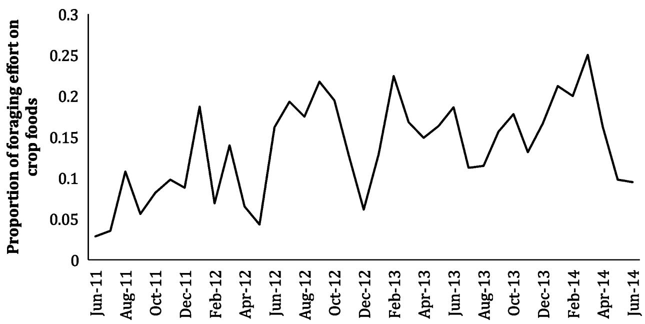

FIGURE 3 Proportion of feeding effort on crop/anthropogenic by vervet monkeys at Nabugabo over 3 years

TABLE 2 Ten foods most frequently consumed by vervet monkeys at Nabugabo over 3 years

Species	Rank	% of total feeding effort (of 100%)
Unidentified Insects	1	9.40
Lantana camara	2	7.19
Pseudospondias spp.	3	7.10
Maesopsis eminii	4	5.29
Ficus natalensis	5	4.16
Pycnathus angolensis	6	3.58
Rauvolfia vomitaria	7	3.05
Syzugium spp.	8	3.05
Elaeis guineensis	9	2.54
Garcinia hillensis	10	2.52

3.4 | Use of crop foods over time, in relation to ecological factors

There was no correlation between feeding effort on crop foods and fruit availability in adjacent forests (F = 0.58, p = .401), nor between feeding time on crop foods and mature crop food availability (F = 0.24, p = .608; Figure 4). However, proportion of feeding effort on crop foods was temporally clustered (Box-pierce test, X = 7.41, p = .006).

4 | DISCUSSION

Contra to our predictions, we did not find any significant differences in macronutrient profiles between wild and anthropogenic foods at Nabugabo. However, proportion of feeding time spent on crop foods was inversely related to proportion of total feeding effort, which supports our prediction that crop foods provide an accessible, nutrient dense package that allows for reduced feeding effort (Hockings, Anderson, & Matsuzawa, 2009; McLennan & Ganzhorn, 2017; Naughton-Treves et al., 1998). We also documented a significant temporal trend in crop raiding by vervet monkeys at Lake Nabugabo; however, this did not correspond to the availability of ripe fruit in nearby forest fragments, or to the availability of ripe crops in the surrounding area.

Analyses of nutrient proportions in crop and wild foods demonstrated macronutrient ratio similarity between wild and crop foods at the extreme ends of the lipid axes. These foods are identified as the anthropogenic oil palm (*Eleanas guinensis*) and wild African nutmeg (*Pycnanthus angolensis*) (with 76% and 70% lipid, respectively). This suggests that the vervet monkeys could be using these resources interchangeably, based on their availability, location or ease of access. If this is the case, cutting down African nutmeg trees for fuelwood or timber might result in increased crop raiding on oil palm. The usage of oil palm by crop-raiding primates is well documented in Africa (i.e., Bryson-Morrison, Matsuzawa, & Humle, 2016; Estrada, Raboy, & Oliveira, 2012), and the expansion of oil palm plantations and monocrops has been identified as a potential threat to primate conservation (Linder & Palkovitz, 2016).

Our finding that feeding effort on crop foods is not correlated to ripe fruit availability is similar to that of Sha and Hanya (2013), who documented that crop raiding in long tail macaques (*Macaca fascicularis*) was opportunistic, such that crop foods were not sought during periods of scarcity, but were consumed when convenient or available. Similarly, Seiler and Robbins (2015) found that mountain gorillas at Bwindi Impenetrable National Park in Uganda also exploited crop and anthropogenic foods opportunistically, with no relationship to food shortages within the park boundaries. This may be the case at Nabugabo as well with crop patches being more advantageous during certain times when crop fields are more accessible (e.g., not guarded). Understanding the relationship between ranging, patch dynamics and variation in crop raiding has implications for management of crop raiding, as it may enable a buffer-zone strategy where conflict mitigation centres around distancing vervet monkeys from available crop fields to lower the feeding advantage (in terms of search time, distance travelled, etc.) to using crop foods.

Alternatively, variation in crop feeding effort could be related to behavioural factors. Strum (2010) found that crop raiding carried different costs among age/sex categories in baboons, leading to differential likelihoods of engaging in crop raiding behaviour. Similarly, Schweitzer, Gaillard, Guerbois, Fritz, and Petit (2017) demonstrated that adult, and particularly adult male, Chacma baboons in Zimbabwe were most likely to initiate collective (group-wide) crop-raiding events. Given that the composition of the vervet monkey group

TABLE 3 Human/crop foods regularly integrated into the top 53 food items (comprising 90% of the diet) in the vervet monkey diet at Nabugabo. Garbage includes a very large range of items thrown into rubbish pits in the group's home range. Feeding effort is the percentage of feeding time devoted to that species divided by the total feeding time

Species	Common name	% of total feeding effort (out of 100%)
Elaeis guineensis	Oil palm	2.54
Manihot esculenta	Cassava	1.73
Psidium guava	Guava	1.3
Mangifera indica	Mango	1.24
Senna siamea	Fuelwood (Cassia)	1.17
Garbage		1.02
Hibiscus sabdariffa	Hibiscus	0.92
Calistamom citrus	Bottlebrush	0.72
Jacaranda	Ornamental	0.68
Ipomea batatas	Sweet potato	0.53
Morus alba	Mulberry	0.51
Zea mays	Maize/corn	0.49
Grevilia robusta	Fuelwood	0.49
Musa paradisiaca	Banana	0.47
Citrus sinensis	Orange	0.38
Abbras precatorias	Seed (for beads)	0.36

observed as a part of this study shifted across the duration of the study, it is possible that some of the variation in mean feeding effort on crop foods (across the whole group) is reflective of group composition and the risks involved in crop raiding. In particular, pregnant or lactating females are less likely to engage in crop raiding because of the high risk of human conflict (Strum, 2010).

Similar to variation in the cost/benefit ratio of crop raiding among group members, feeding effort on crops may be temporally variable based on the intensity of conflict with humans. The anti-crop raiding strategies employed by the community likely vary as a function of perceived intensity of raiding, importance of the planted crop and stage of maturity of the crop (Hill & Wallace, 2012; Naughton-Treves, 1997). Declines in crop raiding have been documented to be associated with persistent human presence in crop fields (i.e., chasing from fields, noisemaking; Hsiao, Ross, Hill, & Wallace, 2013). While we found temporal variability in crop raiding, none of the variables examined related to this pattern of crop feeding. Thus, future work may be helpful in understanding human strategies to mitigate conflict with primates and the implications thereof on the primates' crop-raiding habits.

The nutritional similarities between anthropogenic and wild foods at Lake Nabugabo are intriguing, in suggesting that the contributing factors to crop-raiding behaviours extend beyond nutritional motivators. However, there are greater differences between anthropogenic and wild foods when relative proportions of nutrients, rather than macronutrient composition, is considered. We suggest that future studies consider nutrient balances in addition to macronutrient composition, to elucidate underlying mechanisms that drive the

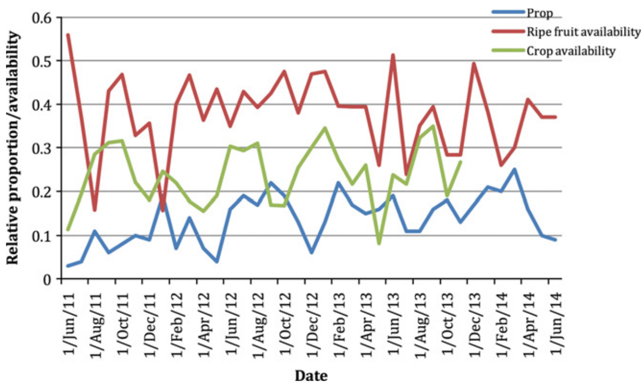

FIGURE 4 Number of crop food scans per month (blue) showed no significant correlation with indices of ripe fruit availability (red) or crop availability (green).

consumption of anthropogenic foods in human-modified landscapes. At Lake Nabugabo, the nutritional similarities between anthropogenic and wild foods indicate that efforts to deter crop raiding and mitigate human–primate conflict should be considered beyond the nutritional perspective (i.e., barriers as opposed to buffer crops).

Lastly, the significant temporal pattern of anthropogenic food usage observed at Nabugabo may be critical to understanding and mitigating human–primate conflict in the region. While seasonality and phenology do not account for differences in crop raiding, the temporal trend suggests that there are ecological or behavioural patterns at play. It has been shown that feeding costs are affected by habitat and home range characteristics (Isbell, Pruetz, & Young, 1998). The availability of crop foods and their large patch size relative to forest foods may encourage crop raiding suggesting that spatial characteristics of crop usage is reflective of changes in ranging behaviour or movement patterns. Previous studies have considered ranging data to understand diet in relation to phenology, range usage and habitat characteristics (Fan & Jiang, 2008; Fashing, 2001; Harris & Chapman, 2007). Such geospatial tools may help uncover new insights into anthropogenic food usage at highly human-modified sites such as Nabugabo, where forest fragments and human settlement are interspersed in a mosaic matrix and ranging proximity may play a large role in the opportunistic consumption of anthropogenic foods.

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SUPPORTING INFORMATION

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