



RESEARCH ARTICLE

Forest fragments become farmland: Dietary Response of wild chimpanzees (*Pan troglodytes*) to fast-changing anthropogenic landscapes

Matthew R. McLennan^{1,2,3} | Georgia A. Lorenti^{1,2} | Tom Sabiiti² | Massimo Bardi⁴¹Department of Social Sciences, Oxford Brookes University, Oxford, UK²Bulindi Chimpanzee and Community Project, Hoima, Uganda³Centre for Ecology and Conservation, University of Exeter, Cornwall, UK⁴Department of Psychology and Behavioral Neuroscience, Randolph-Macon College, Ashland, Tennessee**Correspondence**

Matthew R. McLennan, Bulindi Chimpanzee and Community Project, P.O. Box 245, Hoima, Uganda.

Email: mclennan.bccp@gmail.com

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Abstract

Behavioral flexibility, including an ability to modify feeding behavior, is a key trait enabling primates to survive in forest fragments. In human-dominated landscapes, unprotected forest fragments can become progressively degraded, and may be cleared entirely, challenging the capacity of primates to adjust to the changes. We examined responses of wild chimpanzees (*Pan troglodytes schweinfurthii*) to major habitat change: that is, clearance of forest fragments for agriculture. Over 7 years, fragments in Bulindi, Uganda, were reduced in size by 80%. We compared the chimpanzees' diet at the start and end of this period of rapid deforestation, using data derived mainly from fecal analysis. Similar to other long-term study populations, chimpanzees in Bulindi have a diverse diet comprising over 169 plant foods. However, extensive deforestation seemed to impact their feeding ecology. Dietary changes after fragment clearance included reduced overall frugivory, reduced intake of figs (*Ficus* spp.; formerly a dietary "staple" for these chimpanzees), and reduced variety of fruits in fecal samples. Nevertheless, the magnitude of most changes was remarkably minor given the extent of forest loss. Agricultural fruits increased in dietary importance, with crops accounting for a greater proportion of fruits in fecal samples after deforestation. In particular, cultivated jackfruit (*Artocarpus heterophyllus*) became a "staple" food for the chimpanzees but was scarcely eaten before fragment clearance. Crops offer some nutritional benefits for primates, being high in carbohydrate energy and low in hard-to-digest fiber. Thus, crop feeding may have offset foraging costs associated with loss of wild foods and reduced overall frugivory for the chimpanzees. The adaptability of many primates offers hope for their conservation in fragmented, rural landscapes. However, long-term data are needed to establish whether potential benefits (i.e. energetic, reproductive) of foraging in agricultural matrix habitats outweigh fitness costs from anthropogenic mortality risk for chimpanzees and other adaptable primates.

KEYWORDS

behavioral flexibility, crop feeding, deforestation, foraging adaptations, fragmentation, unprotected habitats

1 | INTRODUCTION

Habitat fragmentation is a leading threat to primate conservation in the tropics (Estrada et al., 2017; Marsh & Chapman, 2013). As natural habitats are converted to other land uses, wild animals including primates are increasingly found in remnant fragments of forest surrounded by mixed agricultural systems, prompting growing interest in the conservation value of such landscapes (Estrada, Raboy, & Oliveira, 2012; Galán-Acedo et al., 2019). Small, disturbed forest fragments generally offer poorer quality habitat compared with continuous forest for most species, and primates inhabiting them typically show feeding adjustments including reduced frugivory and increased reliance on lower-quality foods (e.g. Chaves, Stoner & Arroyo-Rodríguez, 2012; Donati et al., 2011; Tesfaye, Fashing, Bekele, Mekonnen, & Atickem, 2013). Nevertheless, behavioral flexibility, including an ability to modify feeding behavior, has been identified as a key attribute enabling primates to persist in fragmented and other anthropogenically-modified environments (Kalbitzer & Chapman, 2018; McLennan, Spagnoletti, & Hockings, 2017; Nowak & Lee, 2013). In particular, primates may be able to compensate for the poor quality of fragments by supplementing their diet with foods foraged from the surrounding matrix (Anderson, Rowcliffe, & Cowlishaw, 2007; Arroyo-Rodríguez et al., 2017; Asensio, Arroyo-Rodríguez, Dunn & Cristóbal-Azkarate, 2009).

In rural landscapes, agricultural crops are often grown in proximity to forest fragments. Crops offer certain nutritional advantages over some wild foods, that is, being higher in carbohydrate energy and lower in hard-to-digest fiber (Cancelliere, Chapman, Twinomugisha, & Rothman, 2018; McLennan & Ganzhorn, 2017; Schwitzer, Polowinsky, & Solman, 2009), and thus are attractive to many wild animals including primates (Hill, 2017). Recent studies confirm that many primates living in fragmented habitats supplement a natural diet with agricultural foods (e.g. Campbell-Smith, Campbell-Smith, Singleton, & Linkie, 2011; Chaves & Bicca-Marques, 2017; de Freitas, Setz, Araújo, & Gobbi, 2008; Kibaja, 2014; Mekonnen et al., 2012; Moore, Nekaris, & Eschmann, 2010; Pozo-Montuy, Serio-Silva, Chapman, & Bonilla-Sánchez, 2013), a behavior often termed “crop raiding” but which is better described by more neutral terms like “crop foraging” or “crop feeding” (Hill, 2017). Although suggestive of dietary flexibility—and in spite of nutritional benefits—crop feeding is risky, exposing primates to lethal crop protection measures and persecution (McLennan, Hyeroba, Asiimwe, Reynolds, & Wallis, 2012; Paterson, 2005). These risks may be compounded by other hazards that endanger primate survival in matrix habitats, for example, roads, power lines, domestic dogs, and exposure to human or livestock pathogens (Cibot, Bortolamiol, Seguya, & Krief, 2015; Goldberg, Gillespie, & Rwego, 2008; Katsis, Cunneyworth, Turner, & Presotto, 2018; Lindshield, 2016). In addition, fragmented mosaic landscapes are inherently dynamic. Where forest fragments are subject to frequent resource use by local households, they become progressively degraded over time—and may be cleared entirely—impacting the survival of primates in them (Baranga, 2004; Chapman et al., 2013; Chapman, Naughton-Treves, Lawes, Wasserman, & Gillespie,

2007; Wahungu, Muoria, Moinde, Oguge, & Kirathe, 2005). Still, few studies have investigated how primates cope with rapid changes to fragments, including how foraging and other behavioral adaptations might aid or hinder their survival in human-modified landscapes in the long-term (Singh, Kumara, Kumar, & Sharma, 2001).

Like many primates, chimpanzees (*Pan troglodytes*) and other great apes increasingly live in habitats impacted by humans (Hockings et al., 2015; Spehar et al., 2018). Habitat fragmentation and agricultural expansion are linked to chimpanzee population declines throughout tropical Africa (Arcus Foundation, 2015). Nevertheless, chimpanzees show resilience to some habitat modifications, including agriculture, and can persist outside protected areas in fragmented, mosaic landscapes near people, provided they are not heavily hunted (Dunnett, van Orshoven & Albrecht, 1970; Garriga et al., 2019; Hockings & McLennan, 2016; McCarthy et al., 2015; McLennan, 2008). Their diets are broadly omnivorous (e.g., Goodall, 1986; Nishida & Uehara, 1983), but they prefer to eat fleshy fruits (Watts, Potts, Lwanga, & Mitani, 2012a; Wrangham, Conklin-Brittain, & Hunt, 1998). Chimpanzees have been shown to integrate agricultural foods readily into their diets, wherever palatable crops are grown in their habitats (Bessa, Sousa, & Hockings, 2015; Hockings, Anderson, & Matsuzawa, 2009; Krief et al., 2014; McLennan, 2013; Reynolds, Wallis, & Kyamanywa, 2003; Takahata, Hiraiwa-Hasegawa, Takasaki, & Nyundo, 1986). They have been recorded feeding on a variety of cultivated foods across their geographical range, but show a species-typical preference for sugary fruit crops (Hockings & McLennan, 2012). These characteristics make chimpanzees a useful species for examining responses of endangered but flexible wildlife to rapid deforestation in rural tropical landscapes.

In Bulindi, Uganda, chimpanzees (*P. t. schweinfurthii*) inhabit an extensively human-modified habitat comprising small forest fragments, agricultural fields, and villages, 25 km from the nearest continuous forest block, Budongo Forest (McLennan & Hill, 2010; McLennan, Howell, Bardi, & Heistermann, 2019). An earlier study (McLennan, 2013) showed that the chimpanzees' diet in Bulindi was relatively diverse and fruit-dominated, similar to populations in less-disturbed habitats. Figs (*Ficus* spp.) were the most commonly eaten fruit, as determined by fecal analysis. Because their asynchronous fruiting means figs are often available year-round, some authors consider figs a fallback food for chimpanzees, assuming greater importance in their diets when non-fig fruits are scarce (e.g., Harrison & Marshall, 2011). At Bulindi, figs were considered a “staple,” that is, eaten on a daily or near-daily basis year-round. Nevertheless, figs tended to appear in chimpanzee feces in greater quantities when non-fig fruits were scarce, consistent with some qualities of fallbacks (cf. Chancellor, Rundus, & Nyandwi, 2012; Watts, Potts, Lwanga, & Mitani, 2012b). Several agricultural crops were among the most common foods for these chimpanzees, fed on increasingly when wild fruit was scarce in fragments. In particular, cocoa pods from abandoned forest plantations provided an abundant high-quality fallback food when wild fruit availability was low (McLennan, 2013). The chimpanzees foraged for domestic fruits, such as mango, guava,

and papaya, in village areas, with adult males at times showing notably bold, confrontational behavior in their interactions with humans (McLennan, 2010a; McLennan & Hill, 2010). Overall, this earlier study suggested that, despite significant habitat disturbance, the mosaic of human-modified habitats in Bulindi—including the agricultural–village matrix surrounding fragments—offered chimpanzees an assortment of foods year-round.

Here, we examine the dietary response of chimpanzees in Bulindi to major habitat disturbance, that is, conversion of forest fragments to farmland, using data derived primarily from fecal analysis. We collected data ca. 7 years after the first study, during which time most fragments were cleared for farming, and made the following predictions about the chimpanzees' diet following this habitat change:

1. The chimpanzees' diet will be less fruit-dominated, that is, fecal samples will contain less fruit and more lower-quality fibrous plant foods, such as leaves and piths, owing to a reduction in wild fruit trees following extensive clearance of fragments.
2. The chimpanzees' fruit diet will be less diverse, that is, fecal samples will contain fewer fruit species, owing to a potential reduction in the variety or abundance of fruit sources available following extensive clearance of fragments.
3. Figs will feature less prominently in fecal samples, owing to a reduction in fig trees after extensive clearance of fragments.
4. Among wild tree fruits consumed, only fig species have strictly asynchronous fruiting cycles in Bulindi (McLennan, 2010b). Thus, fecal samples will include a lower diversity of seasonal (i.e., non-fig) wild tree fruits, owing to a reduction in trees with seasonal fruit cycles following extensive clearance of fragments.
5. Agricultural crops will feature more prominently in the chimpanzee diet, reflecting a flexible feeding response to loss of wild foods after extensive clearance of fragments.
6. Crop selection by the chimpanzees will show a reduced fruit bias in accordance with the model in McLennan and Hockings (2014), which predicts that animals should show less selectivity in crop feeding with increasing exposure to agriculture.

2 | METHODS

2.1 | Study site

Bulindi (1°29'N, 31°28'E) is situated in Hoima District, western Uganda, midway between the Budongo and Bugoma Forests Reserves—two main forest blocks each inhabited by >500 chimpanzees (Plumptre et al., 2010). Outside these reserves, the landscape is cultivated and densely populated (>150 persons per km²; UBOS, 2016). Nevertheless, a population of ≥260 chimpanzees inhabits unprotected riparian forests across an area of >1000 km² between the reserves (McCarthy et al., 2015). Since the 1990s, the riparian forests were logged and cleared for farming or replaced with exotic timber plantations (Mwau & Witkowski, 2008; Twongyirwe, Bithell,

Richards, & Rees, 2015), leaving only small remnant fragments within an expanding village–agriculture matrix. Linked to these land-use changes, human–chimpanzee interactions have increased markedly (McLennan & Hill, 2012). Close coexistence between villagers and chimpanzees in this landscape is aided by local cultural taboos against hunting primates for food, which enable chimpanzees to persist near villages once the forest has been converted to other land uses (McLennan, 2008). Even so, complaints about crop damage by chimpanzees are widespread (McLennan, 2008), and the survival of chimpanzees regionally is threatened by occasional retaliatory killings and use of snares and steel traps by some farmers to protect crops (McLennan et al., 2012; Reynolds et al., 2003).

The resident chimpanzee group ("community") at Bulindi was first studied in 2006–2008. At that time, the chimpanzees were unhabituated and community size was undetermined; however, there were minimally 25 individuals (McLennan & Hill, 2010). Research resumed in 2012 and is ongoing (McLennan et al., 2019). Between 2012 and 2019 community size has varied from 18 to 22 individuals. The chimpanzees were habituated by 2015. Their home range (ca. 21 km²; McLennan, 2010b) is comprised of small privately-owned forest fragments amid a matrix of agricultural gardens, homes, roads, and trading centers (Figure 1). Cash crops including tobacco, rice, and sugarcane are widely farmed alongside common subsistence crops, for example, maize, cassava, beans, and potato. Fruit trees like mango and jackfruit are commonly grown around homes. Forest fragments occur along streams and around *Cyperus papyrus* swamps and support a mostly groundwater-dependent vegetation community. Common trees include *Phoenix reclinata* palms, *Pseudospondias microcarpa* and members of the Moraceae, for example, *Trilepisium madagascariensis*, *Antiaris toxicaria*, and figs *Ficus* spp. (McLennan & Plumptre, 2012). Regenerating or colonizing forest occurs at forest edges and in small hillside thickets (for a detailed description of forest types at Bulindi, see McLennan & Plumptre, 2012). In the 1960s, farmers established shade cocoa gardens within the riparian forest; these were abandoned in the 1970s–1980s, leaving cocoa as a dominant understory tree. Before recent widespread clearance, riparian forests provided a food-dense habitat for chimpanzees regionally (McLennan & Plumptre, 2012). Rainfall is bimodal with most rain falling between April–May and August–November. Annual rainfall averaged 1461 mm in 2001–2007 (McLennan, 2010b). Daily temperatures reach 33°C and are hottest in the dry months of January–March. For further information about climate and seasonality at Bulindi, see McLennan, Hasegawa, Bardi, and Huffman (2017).

2.2 | Data collection

We explored changes in fragment size and chimpanzee diet in two "periods" separated by an interval of ca. 7 years. From June 2006–January 2008 (corresponding to 'Period 1') main fragments used by the chimpanzees were identified and their areas measured by traversing perimeters on foot using the tracking function of a handheld GPS (McLennan, 2010b). In April–June 2014 (during

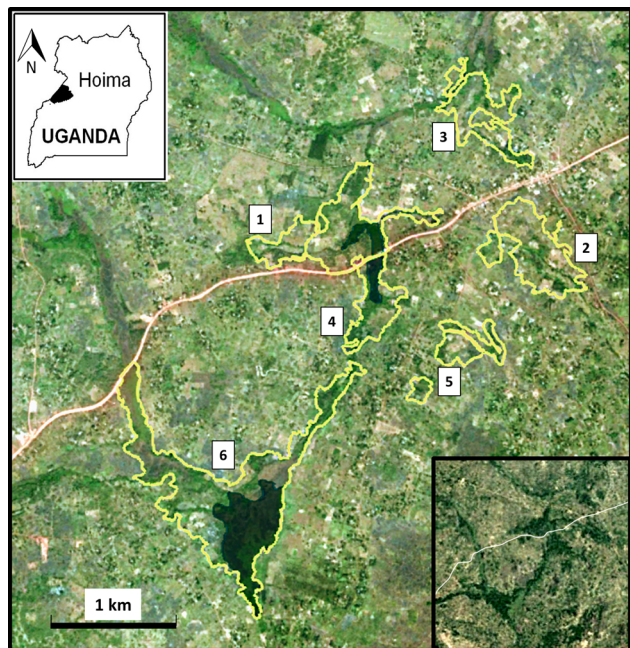


FIGURE 1 Map showing six main forest fragments in the Bulindi chimpanzees' home range (in Hoima District, western Uganda) and changes in fragment size over time; adapted from Google Earth™ 2017. Fragment numbers (1–6) correspond to Table 1. *Main map:* Base map imagery depicts land cover in January 2017, that is, one year after Period 2 (imagery was not available for 2014–2015 due to cloud cover; however, little change in forest cover occurred after 2015). Light green areas show the remaining patches of riparian forest. Dark green expanses within fragments 1, 4, and 6 are papyrus swamps (i.e., not forest). Outer yellow outlines show the perimeter of each fragment in Period 1. The surrounding matrix is a patchwork of agricultural fields and village homes. Trading centers are located along the main road (at center), which connects Hoima and Masindi towns. *Inset* (lower right corner): Map of Bulindi from 1985 showing the riparian forests (dark green) before extensive clearance

'Period 2', which corresponds to January 2014–December 2015), we remeasured these same fragments. Significant forest clearance in Bulindi predates our research there by at least 5 years. However, by Period 1 all fragments were being logged and converted to farmland (McLennan, 2010b). Deforestation continued steadily to 2014. By 2015 most clearances stopped owing to conservation incentives and because most remaining areas of forest were swampy and unsuitable for agriculture. Thus, by Period 2 remaining forest was greatly reduced in size, highly degraded, and with many large trees removed.

To understand how this situation impacted the chimpanzees, we compared their diet in each study period. In Period 1 the chimpanzees were unhabituated, which precluded using direct observation to explore feeding behavior. Therefore we used systematic fecal analysis to describe their diet (McGrew, Marchant, & Phillips, 2009). Although fruit and insect residues are often identifiable in feces, macroscopic fecal analysis is less useful for assessing nonfruit plants eaten because foliage items like leaves and piths are rarely identifiable taxonomically (Phillips & McGrew, 2013). Even so, the relative amount of fruit to nonfruit plant parts in feces is

quantifiable (McLennan, 2013). In support of this approach, Phillips and McGrew (2014) showed that quantified proportions of fruit and nonfruit plants in chimpanzee feces were valid proxy measures of time individuals spent feeding on fruit and foliage.

In Period 1, fecal sampling was conducted over 13 consecutive months (January 2007–January 2008; $n = 1,436$ "dungs"; see McLennan, 2013). Here, we present comparative data on the chimpanzee diet from Period 2, after a further 6–7 years of continuous deforestation. Although the chimpanzees became habituated during Period 2 (McLennan et al., 2019) and could be observed feeding directly, we used data from fecal analysis to allow comparison with Period 1. Chimpanzee dungs ($n = 482$) were collected over 14 months in 2014–2015, between January–April and September–November 2014, and March–June and October–December 2015. Duplicate months, that is, March–April and October–November, which were covered in both years, correspond generally to high and low fruit seasons in Bulindi, respectively; the two calendar months not covered by fecal sampling in Period 2 (July–August) correspond to an intermediate to low fruit season (McLennan, 2013; and unpublished data).

In both periods, we collected fresh (≤ 24 hr old) chimpanzee dungs from beneath night nests and during daily tracking. Only one dung specimen was collected per night nest. If successive dung piles (e.g., along trails) were judged to originate from the same individual based on the similarity of appearance and age, only one specimen was collected. Macroscopic fecal analysis was carried out as described in McLennan (2013). Briefly, we rinsed dungs through a 1-mm sieve and, once dry, estimated the volume percentage of all fruit (seeds, skins, pulp), fig fruit separately, nonfruit plant parts (piths, leaves, bark), and nonplant "other" items at 5% intervals with respect to the total mass of undigested content. Most fruit remains could be identified to species-level by the seeds, though figs were lumped since the seeds are not distinguishable macroscopically. Although the chimpanzees eat insects and their products occasionally (McLennan, 2014), invertebrates comprise a trivial fraction of dung content overall, whereas vertebrate consumption is negligible at Bulindi (Cibot, Sabiiti, & McLennan, 2017). The mean volume % of "other" (mostly insect) remains in dungs was 0.9% and 0.8% in Periods 1 and 2, respectively, and did not differ between periods (Mann–Whitney $U = 338135$; $p = .13$). Therefore, the inverse of the fruit content in dungs is the nonfruit plant content (mostly piths and leaves), which serve a fallback role for chimpanzees in Bulindi (McLennan, 2013). Plants were identified by botanists at Makerere University Herbarium, Uganda. A reference collection of seeds aided the identification of seeds in chimpanzee feces.

We distinguished cultivated foods and exotics ("crops"), which are ordinarily planted and tended to by people, from "wild" foods, accepting that crops occasionally occur as naturalized or abandoned specimens (e.g., guava) as well as in agricultural gardens and around homes. For each dung, we scored six indices of dietary content: (1) "% fruit" to measure overall frugivory, with the amount of fruit relative to nonfruit plants providing an index of diet quality; (2) "% fig" to evaluate the contribution of figs in the diet; (3) the total "number of different fruits" found in the dung (whether wild or crops) to assess the diversity

of the fruit diet; (4) the “number of non-fig wild tree fruits” found in the dung as a measure of the diversity of seasonally available fruits in forest fragments; (5) the “number of different fruit crops” found in the dung to assess the diversity of agricultural fruits eaten; and (6) the “% crop fruits”, which is the percentage of the different fruits found in the dung that are cultivated, thus measuring the representation of agricultural crop fruits eaten relative to wild fruits.

As with wild foods, a drawback to using fecal analysis to study crop feeding by primates is that it underestimates the consumption of nonfruit crops (e.g., sugarcane). In addition, certain crop fruits lack identifiable seeds (banana) or have large seeds that are not normally ingested (jackfruit, mango). At Bulindi, such crop fruits were normally identifiable in feces by the presence of undigested fruit pulp (which could dominate dung content) and/or characteristic fibers (mango) (McLennan, 2013). To explore the chimpanzees' use of nonfruit crops and help identify potential changes in crop feeding between periods, we supplemented fecal data with information from fresh feeding traces (≤ 24 -hr old), which are not biased towards fruit (Doran et al., 2002). Feeding traces were assigned to chimpanzees on the basis of species-typical manner of processing and/or associated sign (e.g., dung, knuckle marks), or following direct observations of chimpanzees feeding on the item (McGrew, Baldwin, & Tutin, 1988). For a given food, multiple same-age feeding traces found in close proximity (within ca. 200 m) were treated as a single data point. The number of feeding traces considered was 369 in Period 1 and 513 in Period 2. Food traces were recorded opportunistically; thus we did not include these data in our analysis.

2.3 | Data analysis

First, we assessed the extent of forest loss by comparing sizes of forest fragments in the chimpanzees' home range in Periods 1 and 2. Next, we compiled an updated list of plant foods recorded in the chimpanzee diet at Bulindi from 2007 (McLennan, 2013) to the present (2019) to assess overall dietary diversity, compiling data from fecal analysis, food traces, and direct observations.

To evaluate the chimpanzees' dietary response to clearance of forest fragments between Periods 1 and 2, we used a multivariate analysis of variance (MANOVA) including as response variables the six dietary indices obtained from the fecal analysis: % fruit content of dungs; % fig content of dungs; no. different fruits per dung; no. different wild (non-fig) tree fruits per dung; no. different agricultural crop fruits per dung; and the % of different fruits per dung that are crops. We chose to run a MANOVA to assess differences between the periods across all response variables simultaneously to avoid running multiple tests on the same data set. However, all variables were nonnormally distributed, displaying either positive or negative skewness (ranging from -1.56 to 1.39). Efforts to normalize the data using standard transformations (logarithmic and trigonometric functions) did not return satisfactory results. Considering that deviations from normality do not have a significant effect in most large samples (Altman & Bland, 1995), we decided to proceed with the MANOVA in the absence of normality given our large sample size ($n = 1,918$ dungs).

To confirm this choice, we ran preliminary univariate *t*-tests and equivalent nonparametric Mann-Whitney *U* tests to test for differences in the six response variables between periods, and compared the results (Table S1). The nonparametric tests returned results for all variables below $p < .05$, whereas *t*-tests were below this threshold for 5 of the 6 variables, thus confirming that using parametric tests did not increase the probability of Type I error. Because most dungs were collected anonymously (i.e., the depositor's identity was unknown), and individual chimpanzees will have contributed multiple fecal samples, nonindependency might have been a problem in our data set. We, therefore, tested for autocorrelation and partial correlation using a Durbin-Watson autocorrelation test, which calculates the residuals from a set of data using a least square regression: $e_t = \rho e_{t-1} + \varepsilon$, where t is the iteration, and ρ the autocorrelation, and ε is the error. When $\rho = 0$ (no autocorrelation), the related statistic is equal to 2. The D-W statistic returns a value between 0 and 4; values between 1.5 and 2.5 suggest that autocorrelation is not a concern. In our sample the D-W statistic was 1.38, indicating moderate positive autocorrelation. This is unsurprising since members of the chimpanzee community have similar diets at a given time of year. However, because there was no way to estimate the potential error introduced by this autocorrelation, we decided to increase the threshold for significance from $p < .05$ to $p < .01$, thus using a conservative approach to minimize Type I error (Chatterjee & Simonoff, 2013). We used univariate between-subject ANOVAs as post hoc tests in our model to assess the individual effect of the six dietary response variables. With the exception of normality, all other assumptions for MANOVA were verified.

Next, we created a discriminant function to assess to what extent we can predict whether a given fecal specimen came from Period 1 or 2, on the basis of our six measures of diet content. The categorical variable “period” was entered as the nonmetric criterion and the six metric dietary response variables as predictors. An optimal discriminant function would allocate $>80\%$ of dungs correctly to Period 1 or Period 2 on the basis of overall dietary content as measured by the predictor variables (Johnson & Wichern, 2002), thus lending support to our hypothesis that the chimpanzees' diet would differ markedly between periods. Finally, we used a Chi square test to assess whether the frequency of dungs containing figs differed between periods. All analyses were performed using SPSS Version 25.0 (SPSS Inc., Chicago, IL), and all tests were two-tailed.

This research involving wild chimpanzees was noninvasive and adhered strictly to the legal requirements of Uganda and to ethics guidelines detailed by the Association for the Study of Animal Behaviour (UK) and the American Society of Primatologists Principles for the Ethical Treatment of Nonhuman Primates.

3 | RESULTS

3.1 | Decrease in size of forest fragments

The chimpanzees used six main forest fragments in Period 1, ranging in size from 14 to 50 ha (Table 1; Figure 1). The change in fragment

TABLE 1 Decrease in size of main forest fragments in Bulindi between surveys made in Period 1 and Period 2^a

Forest fragment	Forest type	Size (ha) in Period 1	Size (ha) in Period 2	% Reduction
Main fragments measured in both surveys				
1. Kyamaleera ^b	Riparian/swamp	37.8	12.5	66.9%
2. Kiseeta	Riparian	29.4	1.8	93.9%
3. Kaawango	Riparian/swamp	24.1	1.8	92.5%
4. Kyamusoga ^b	Riparian/swamp	16.3	9.9	39.3%
5. Katigiro ^c	Hillside	14.0	Cleared by 2014	ca. 100%
		Total: 121.6 ha	Total: 26.0 ha	78.6%
Other main fragment				
6. Mparangasi-Nyakakonge ^d	Riparian/swamp	49.9	Not measured in full	>50%

^aForest surveys were made between June 2006 and January 2008 (Period 1) and in April–June 2014 (during Period 2).

^bArea estimates for the Kyamaleera and Kyamusoga fragments include 3.6 ha and 2.7 ha of *Cyperus papyrus* swamp in both surveys, respectively.

^cNot surveyed in Period 2 because the forest was virtually cleared and no longer offered habitat or cover for chimpanzees.

^dDuring Period 1, the “Mparangasi–Nyakakonge” fragment consisted of a 2 km stretch of riparian forest that adjoined an expanse of swamp forest (combined area = 49.9 ha); only a portion of the riparian forest was remeasured in Period 2. However, extensive clearance (estimated at more than 50%) had occurred by Period 2, including near-total clearance of the swamp forest portion of the fragment.

size between periods was quantifiable for five fragments. These declined in combined size from 121.6 ha in Period 1 to 26.0 ha in Period 2, a loss of 78.6% in 7–8 years (Table 1). The average decrease in the size of individual fragments was similarly 78.5% (range: 39.3–100%). Two riparian fragments were reduced by more than 90% between surveys and had been largely abandoned by chimpanzees by Period 2, whereas a hillside fragment had been effectively cleared and no longer offered habitat for the chimpanzees. A sixth main fragment was only partially remeasured in Period 2, and thus the decrease in forest area between surveys could not be quantified. Certainly, however, less than 50% remained by Period 2. Besides these main fragments, several other smaller forest patches and ecotone thickets used occasionally by chimpanzees in Period 1, but not measured in either survey, were partially or entirely cleared by Period 2.

3.2 | Dietary changes between periods

Chimpanzees at Bulindi have a diverse plant diet with 169 items from 119 identified plants recorded eaten since research began (Appendix). Their full dietary repertoire is larger, however, since not all plants eaten have been formally identified. Moreover, plant foods were still being newly recorded in 2019. Many items are uncommonly eaten: that is, 17.2% of items were recorded fed on once only. Although most confirmed foods were fruits in Period 1, when dietary data derived mainly from fecal analysis, nonfruit plants—especially leaves and piths—have a much greater representation in the updated food list, owing to increased observations of foliage consumption once chimpanzees became habituated in 2015 (Appendix). Fifteen crop species feature in the food list. A large majority (89.3%) of plant foods are “wild” ($n = 151$ items) as opposed to cultivated ($n = 18$ items). The chimpanzees have been observed eating figs from 10 species of *Ficus*.

The MANOVA confirmed that the chimpanzees’ diet varied markedly from Period 1 to Period 2 (MANOVA: Pillai’s trace = 0.136; $F_{6,1909} = 50.2$, $p < .0001$). Thus, clearance of forest fragments appeared to influence their overall diet. Even so, the partial eta squared (ϵ^2) of this main effect was 0.14, indicating that only 14% of the variance in the data set was explained by period.

Post hoc univariate ANOVAs revealed changes in diet for five of the six dietary variables (Figure 2a,b). Average fruit content (% fruit) in chimpanzee dungs declined moderately from $81.6\% \pm 0.49$ (mean \pm SE) in Period 1 to $77.6\% \pm 1.03$ in Period 2 ($p < .0001$). Because the inverse of fruit content in dungs is the nonfruit plant content, this suggests the chimpanzees ate more foliage foods (leaves and piths) in Period 2. The proportion of individual dungs comprising fig residue (% fig) was on average nearly twice that in Period 1 ($21.8\% \pm 0.59$) compared with Period 2 ($11.7\% \pm 0.49$; $p < .0001$). The chimpanzees’ fruit diet was somewhat more diverse in Period 1 when dungs contained residues of 3.76 ± 0.41 different fruits on average, compared to 3.49 ± 0.07 in Period 2 ($p = .001$). Both measures of agricultural crop consumption indicated that cultivated fruits increased in dietary importance in Period 2 (Figure 2a,b). The mean number of different crop fruits in dungs increased from 0.96 ± 0.02 in Period 1 to 1.28 ± 0.04 in Period 2 ($p < .0001$), whereas the percentage of the different fruits in dungs that were crops increased from $24.4\% \pm 0.55$ in Period 1 to $37.4\% \pm 1.12$ in Period 2 ($p < .0001$). Only the number of different wild, seasonal tree fruits in dungs showed no change between periods (Period 1 = 0.94 ± 0.02 ; Period 2 = 1.01 ± 0.04 ; $p = .12$; Figure 2b).

The best discriminant function model ($\chi^2_6 = 280.07$, $p < .001$) classified 1,495 of the 1,918 dungs correctly (77.9%), according to the period they were collected (Tables S2 and S3). The discriminant function was very accurate in classifying dungs from Period 1 (1,377 of 1,436 dungs classified correctly = 95.9%), but rather inaccurate for dungs from Period 2 (118 of 482 dungs classified correctly = 24.5%).

Table 2 lists fruits most commonly appearing in fecal samples in each study period. Overall, there was considerable overlap in

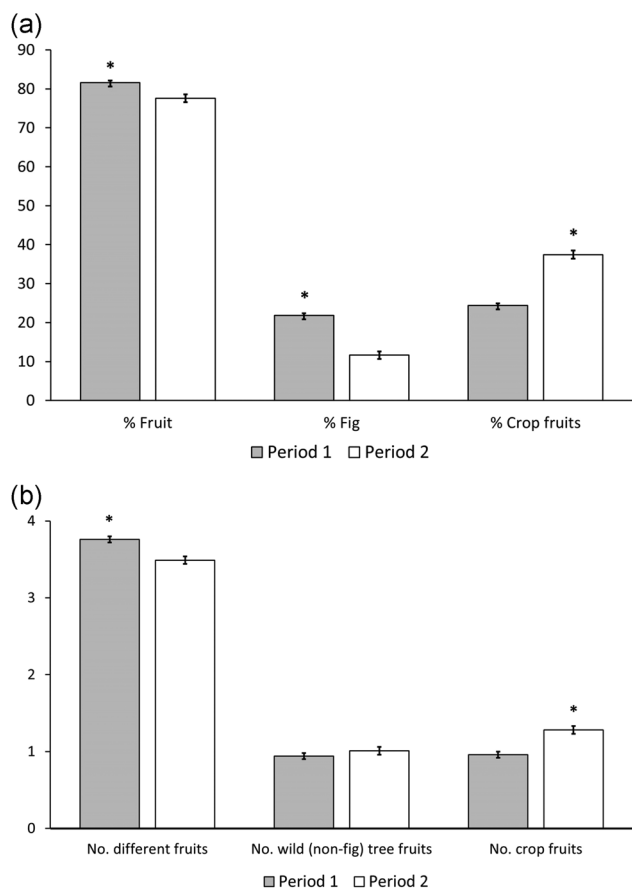


FIGURE 2 Changes in the chimpanzee diet at Bulindi between periods according to six indices of diet content (Period 1: gray bars, $n = 1,436$ dungs; Period 2: white bars, $n = 482$ dungs). (a) “% fruit” is the mean volume % fruit content in dungs (note that the inverse of fruit content is the nonfruit plant content, i.e., foliage); “% fig” is the mean volume % fig content in dungs; “% crop fruits” is the mean percentage of the different fruit species per dung that were agricultural crops. (b) ‘No. different fruits’ is the mean number of different fruit species (wild and cultivated) per dung; ‘No. wild (non-fig) tree fruits’ is the mean number of different seasonally available tree fruit species in dungs; ‘No. crop fruits’ is the mean number of different agricultural crop fruits in dungs. Errors bars represent 95% coefficient intervals ($2 \times \text{SEM}$). (*) indicates a difference between periods of $p < .01$

common fruit foods. Asynchronously fruiting figs occurred in 86.6% of dungs in Period 1 and were the “top-ranked” fruit. In Period 2 figs were second-ranked, occurring in 59.8%. The difference in the frequency of figs in dungs was significant ($\chi^2 = 162.19$, $df = 1$, $p < .0001$). Concerning seasonal wild tree fruits, whereas seeds of some species occurred more commonly in dungs in Period 1 (e.g. *Caloncoba crepiniana* and *Antiaris toxicaria*), others were more common in Period 2 (*Pseudospondias microcarpa* and *Morus mesozygia*).

Concerning crops, the chimpanzees ate guava fruit in all months in both periods. Guava was the “top-ranked” fruit in Period 2 and second-ranked (after figs) in Period 1 (Table 2). The most notable change, however, was the appearance of jackfruit as a common food in Period 2, whereas it was not observed in dungs in Period 1 (Table 2).

Evidence from feeding traces provided supplementary information about agricultural crops eaten. Table 3 lists crops eaten in each period and their importance in the chimpanzee diet, as suggested by feeding trace evidence compared to systematic fecal analysis. Traces of fleshy fruit crops (i.e., containing sugary pulp) were most commonly recorded in both periods. Overall, more nonfruit crops were recorded in Period 2 (Table 3). Although common crop food traces were similar in both periods, two main differences are apparent. Cocoa and jackfruit were the most commonly encountered traces in Periods 1 and 2, respectively. Cocoa accounted for 43.4% of all crop food traces in Period 1, with traces recorded mainly in abandoned forest plantations. By Period 2, the forest plantations had been cleared and cocoa accounted for only 2.7% of crop food traces. Conversely, jackfruit was barely eaten in Period 1 (0.9% crop traces) but was a “staple” food by Period 2, eaten most days (47.5% crop traces; Table 3).

4 | DISCUSSION

The fate of small, unprotected forest fragments in Bulindi is illustrative of wider land-use changes occurring regionally (Mwavu & Witkowski, 2008; Twongyirwe et al., 2015) and elsewhere in Uganda (Baranga, 2004; Chapman et al., 2007, 2013). Although the historic extent of forest cover in Bulindi is uncertain, forests were likely confined to riparian valleys and hillsides. In the 1960s, shade cocoa gardens were established under forest canopy, potentially marking the onset of significant forest disturbance in recent times (McLennan, 2010b). Satellite imagery available from Google Earth™ indicates that as recently as the 1980s main fragments were connected along watercourses (Figure 1, inset). Still, by Period 1, the chimpanzees had already experienced substantial habitat change and showed behavioral adjustments to this situation, for example by incorporating agricultural crops in their seasonal foraging strategies (McLennan, 2013), and displaying markedly bold or confrontational behavior towards humans (McLennan, 2010a, 2010b; McLennan & Hill, 2010). Nevertheless, the dramatic forest loss that occurred between Periods 1 and 2—almost 80% in just 7 years—is expected to present significant challenges even to a highly flexible species like chimpanzees.

Chimpanzees in Bulindi have an overall diverse diet, similar to other long-term study populations including those in markedly less-disturbed habitats, which typically consume parts of >100 plant species (Goodall, 1986; Nishida & Uehara, 1983; Tutin & Fernandez, 1993; Watts et al., 2012a). Our findings revealed a change in the chimpanzees’ diet in the two study periods. Although we did not quantify changes in the number and phenology of feeding trees in the diminished fragments, the loss of such a large proportion of core forest habitat between periods evidently represents a reduction in wild food trees available to the chimpanzees, and it is a fact that most former fruit trees were no longer present by Period 2 (personal observations). Thus, the extensive deforestation seemed to impact their feeding ecology, and most of our predictions were broadly

TABLE 2 Fruits most commonly appearing in chimpanzee fecal samples (>5% dungs) at Bulindi in Period 1 and Period 2

Period 1 (McLennan, 2013)			Period 2		
Plant fruit species	Life form ^a	% Dungs ^b	Plant fruit species	Life form ^a	% Dungs ^b
1. <i>Ficus</i> spp. [†]	T	86.6	1. <i>Psidium guajava</i> [‡] (guava)	T	66.2
2. <i>Psidium guajava</i> [‡] (guava)	T	50.5	2. <i>Ficus</i> spp. [†]	T	59.8
3. <i>Phoenix reclinata</i>	T [§]	43.9	3. <i>Pseudospondias microcarpa</i>	T [§]	39.0
4. <i>Aframomum</i> spp. [†]	H	27.0	4. <i>Artocarpus heterophyllus</i> [‡] (jackfruit)	T	38.8 (Period 1: 0%)
5. <i>Monanthotaxis ferruginea</i>	C	19.8	5. <i>Phoenix reclinata</i>	T [§]	34.7
6. <i>Mangifera indica</i> [‡] (mango)	T	17.8	6. <i>Morus mesozygia</i>	T [§]	12.0 (Period 1: 4.4%)
7. <i>Carica papaya</i> [‡] (papaya)	T	14.1	7. <i>Lantana camara</i>	S	11.4
8. <i>Pseudospondias microcarpa</i>	T [§]	13.0	8. <i>Aframomum</i> spp. [†]	H	10.8
9. <i>Theobroma cacao</i> [‡] (cocoa)	T	12.3	9. <i>Dovyalis macrocalyx</i>	S	10.6
10. <i>Caloncoba crepiniana</i>	T [§]	11.7 (Period 2: 0%)	10. <i>Parkia filicoidea</i>	T [§]	10.4
11. <i>Rubus pinnatus</i>	S	10.7 (Period 2: 2.5%)	11. <i>Monanthotaxis ferruginea</i>	C	10.2
12. <i>Parkia filicoidea</i>	T [§]	9.8	12. <i>Mangifera indica</i> [‡] (mango)	T	7.7
13. <i>Coccinia</i> sp.	C	8.6 (Period 2: 1.5%)	13. <i>Carica papaya</i> [‡] (papaya)	T	7.3
14. <i>Dovyalis macrocalyx</i>	S	8.4	14. <i>Theobroma cacao</i> [‡] (cocoa)	T	5.8
15. <i>Lantana camara</i>	S	6.4			
16. <i>Antiaris toxicaria</i>	T [§]	5.9 (Period 2: 0.8%)			

Note: Fruits are ranked in descending order of importance in the diet in each period, according to fecal analysis.

^aLife form: T, tree; H, herb; C, climber (liane or vine); S, shrub.

^bPercentage of chimpanzee fecal samples (dungs) containing identifiable residues of each fruit food (i.e., seeds, skins and or pulp). For fruits that were common (>5% dungs) in one period only, the corresponding percentage value for the other period is shown in parenthesis for comparison; Period 1 = 1,436 dungs, Period 2 = 482 dungs (see Methods for dates covered by each period).

[†] = comprises multiple species of a genus.

[‡] = cultivated crop.

[§] = seasonally available (non-fig), wild tree fruit.

supported. Nevertheless, the magnitude of changes observed was lower than expected.

The fruit component of dungs declined between periods, indicating reduced frugivory and greater intake of lower-quality foliage items (piths and leaves) (prediction 1), while dungs also contained fewer different fruits in Period 2 (prediction 2). Although potentially suggestive of a decline in habitat-wide fruit availability, these differences were remarkably minor: average fruit content of dungs dropped from 82% in Period 1 to 78% in Period 2, whereas the number of different fruits in dungs declined from 3.8 to 3.5, respectively. Thus, the chimpanzees continued to have a relatively diverse diet dominated by fruit, despite the loss of most natural forest in their range. McLennan and Plumptre (2012) proposed that a high density of figs, which fruit asynchronously in Bulindi, may help explain the occurrence of chimpanzees in riparian forests regionally. Although figs remained an important dietary component in Period 2, figs appeared in dungs considerably less often and in lesser quantities compared to Period 1 (prediction 3). Remaining figs in fragments continued to fruit asynchronously during Period 2 (personal observations), but additional data are needed to determine if figs remained at sufficient density to offer a reliable fallback for chimpanzees when seasonal fruits were scarce (cf. Chancellor et al., 2012). The moderate decline in fruit intake between periods suggests they might not have.

Contrary to prediction 4, there was no change in the number of seasonal tree fruits in dungs between periods. This was surprising because many large fruit-bearing trees had been removed by Period 2. Consequently, we anticipated the chimpanzees would rely more heavily on nontree fruits, such as from climbers, shrubs, and herbs but that was not the case (Table 2). Thus, despite the loss of trees from ca. 80% of forest area used by the chimpanzees in Period 1, they continued to feed on a similar variety of seasonal forest tree fruits. Though statistically significant, our model had relatively poor predictive power—only 14% of the variance in dung content was explained by period—suggesting that additional factors were involved, particularly phenology. Although fecal sampling in Period 1 covered 13 consecutive months, in Period 2 sampling was conducted over 2 years and not all calendar months were covered (see Methods). Consequently, differences between periods in frequencies of some seasonal fruits in dungs might relate to phenology patterns. For example, sampling covered two fruiting cycles of *Pseudospondias microcarpa* in Period 2 (personal observations), but only one during Period 1, when it occurred in a smaller proportion of fecal samples (Table 2). Still, reduced consumption of some other seasonal tree fruits in Period 2 likely relates to loss of most mature specimens (e.g., *Antiaris toxicaria* and *Caloncoba crepiniana*). Additional research is required to establish current densities of fruit tree species in remaining forest patches, including phenology studies to help quantify the reduction in wild fruit

TABLE 3 The importance of individual cultivated crops/exotics in the chimpanzee diet at Bulindi in Period 1 and Period 2, as suggested by two methods: Systematic fecal analysis and (nonsystematic) feeding traces

Crop food item ^a	Part eaten ^b	Period 1			Period 2		
		% dungs ^c	% food traces ^d	% crop food traces ^e	% dungs ^c	% food traces ^d	% crop food traces ^e
Fleshy fruits							
<i>Artocarpus heterophyllus</i> (jackfruit)	Fruit ^{R, UR}	0	0.5	0.9	38.8	23.8	47.5
<i>Carica papaya</i> (papaya)	Fruit ^{R, UR}	14.1	4.1	6.8	7.3	2.9	5.8
<i>Citrus limon</i> (lemon)	Fruit ^{R, UR}	– ^f	–	–	0.4	0.2	0.4
<i>Citrus sinensis</i> (orange)	Fruit ^R	0	1.9	3.2	0	0.6	1.2
<i>Mangifera indica</i> (mango)	Fruit ^{R, UR}	17.8	6.0	10.0	7.7	5.8	11.7
<i>Musa</i> spp. (banana)	Fruit ^{R, UR}	0.9	3.8	6.3	0	0.6	1.2
<i>Passiflora</i> spp. (passion fruit)	Fruit ^R	0.3	0.8	1.4	2.3	0	0
<i>Psidium guajava</i> (guava)	Fruit ^{R, UR}	50.5	3.0	5.0	66.2	7.6	15.2
<i>Solanum betacea</i> (tamarillo)	Fruit ^R	0	0.3	0.5	–	–	–
<i>Theobroma cacao</i> (cocoa)	Fruit ^{R, UR}	12.3	26.0	43.4	5.8	1.4	2.7
Non-fleshy fruits							
<i>Dioscorea alata</i> (yam)	Leaf	–	–	–	0	0.2	0.4
<i>Dioscorea alata</i> (yam)	Pith/stem	0	0.3	0.5	0	0.8	1.6
<i>Eucalyptus</i> sp. (eucalyptus)	Pith/stem	–	–	–	0	0.2	0.4
<i>Musa</i> spp. (banana)	Pith/stem	0	2.4	4.1	0	3.5	7.0
<i>Phaseolus vulgaris</i> (beans) [†]	Fruit ^{UR}	–	–	–	0.8	0	0
<i>Saccharum officinarum</i> (sugarcane)	Pith/stem	0	10.8	18.1	0	2.1	4.3
<i>Zea mays</i> (maize)	Pith/stem	–	–	–	0	0.4	0.8

^aCrops are categorized as “fleshy fruits” (containing soft, sugary pulp) and “non-fleshy fruits” (i.e., pith/stems and leaves), following McLennan and Hockings (2014).

^b“R” and “UR” indicate that the fruit or seed/pod may be eaten ripe and/or unripe, respectively.

^cValues show the percentage of fecal samples (dungs) in which each crop food item was recorded: Period 1 = 1,436 dungs; Period 2 = 482 dungs (see Methods for dates covered by each period).

^dValues show the percentage contribution of each crop food to all feeding trace records (wild foods and crops combined) in each period: Period 1 = 369 traces; Period 2 = 513 traces.

^eValues show the percentage contribution of each crop food to all crop feeding traces (crops only) in each period: Period 1 = 221 traces; Period 2 = 257 traces.

^fDashes indicate the item was not recorded eaten by chimpanzees during the period by any method (fecal analysis, feeding traces, or direct observation).

[†]Although bean pods are botanically fruits, they are categorized here as “non-fleshy fruits” since the pods lack soft, fleshy pulp.

availability since Period 1 (cf. McLennan, 2010b). Still, the inability of the discriminant function to classify dungs from Period 2 correctly (while, conversely, it proved accurate at classifying dungs in Period 1) may hint at the uncertainty of feeding choices for chimpanzees after fragment clearance. In Period 1, dungs consisted mostly of wild fruit residues, with foliage and crop fruits appearing in appreciable amounts only when seasonal tree fruits were scarce (McLennan, 2013). In contrast, in Period 2 leaves, piths, and crop fruits could dominate individual dungs at any time of year.

As expected (prediction 5), agricultural fruit assumed greater dietary importance for the chimpanzees after clearance of fragments, helping to explain how they were able to maintain a fruit-dominated diet. Previous work showed that chimpanzees exposed to agriculture integrate crops in their diets strategically, targeting preferred seasonal crops when available, but increasing overall crop consumption during wild food shortages (Hockings et al., 2009; Krief et al., 2014;

McLennan, 2013; Naughton-Treves, Treves, Chapman, & Wrangham, 1998). Our study indicates that wild chimpanzees respond to removal of wild foods by relying increasingly on human foods. Similar behavioral adjustments to deforestation are shown by chimpanzees elsewhere regionally, including a shift to nesting in exotic timber plantations (McCarthy, Lester, & Stanford, 2017). The energetic benefits of crop feeding for chimpanzees (McLennan & Ganzhorn, 2017) and other primates (Cancelliere et al., 2018) may be sufficient to offset foraging costs associated with reduced intake of wild fruit and perhaps also physiological “stress” associated with chronic human disturbance (i.e., elevated glucocorticoid secretions; McLennan et al., 2019).

Finally, we found only limited support for prediction 6: that crop choice would become more omnivorous (less fruit-biased), according to the model in McLennan and Hockings (2014). In support of this prediction, more nonfruit crops were recorded eaten in Period 2.

Yet although some nonfruit items (e.g., maize pith, bean pods) were potentially recent dietary additions, acquired since Period 1, they were evidently rare foods in Period 2 (Table 3) and similar low levels of consumption might have been missed in Period 1. In fact, the nonfruit crops eaten most often were the same in both periods, that is, sugarcane and banana pith (Table 3).

Undoubtedly, the most salient change in the chimpanzees' crop feeding relates to a single crop: jackfruit (*Artocarpus heterophyllus*). Jackfruits are the largest tree-borne fruit and the pulp contains high levels of digestible sugars (McLennan & Ganzhorn, 2017). A single jackfruit can satisfy multiple chimpanzees (Figure 3). Jackfruit trees are common in village gardens and compounds in Bulindi, yet in Period 1 the chimpanzees largely ignored this high-quality resource. By Period 2, jackfruit was eaten ripe and unripe year-round, and thus had become a "staple" food for this community. The switch to eating jackfruit was not an artifact of habituation (i.e., by making the chimpanzees bolder and more willing to enter "risky" village areas) since in Period 1 when they were unhabituated, they ate other crops foraged from around village homes and gardens, for example, mango, papaya, banana, guava, and sugarcane (McLennan, 2010a, 2010b). Neither is the change related to availability; most large jackfruit trees favored by the chimpanzees are decades old. Rather, habitual jackfruit feeding coincides with the extensive clearance of fragments between Periods 1 and 2. This includes clearance of the abandoned forest cocoa plantations, which, like figs, provided a year-round food source for the chimpanzees (McLennan, 2013); by Period 2 only a small number of naturalized cocoa trees remained within fragments.

4.1 | Primate survival in dynamic human-dominated landscapes

Faced with rapid habitat change, wild chimpanzees in Bulindi adjusted their behavior and ecology to new environmental conditions. Our study, therefore, adds to our expanding knowledge of the behavioral flexibility and ecological resilience of great apes and other primates in response to human disturbances, including deforestation and fragmentation (Hill, 2017; Hockings et al., 2015; Kalbitzer & Chapman, 2018; McKinney, 2019; McLennan, Spagnoletti et al., 2017; Mekonnen et al., 2018; Nowak & Lee, 2013; Spehar et al., 2018). Although this adaptability offers some hope for primate conservation in changing landscapes (McLennan, Spagnoletti et al., 2017), data suggest that human-caused mortality risk (e.g., from persecution, vehicle collisions, electrocutions, and domestic dogs) impacts primate survival in matrix habitats (Hetman, Kubicka, Sparks, & Tryjanowski, 2019; Katsis et al., 2018; Kibaja, 2014; Lindshield, 2016; Moore et al., 2010; Paterson, 2005; Waters, El Harrad, Chetuan, Bell, & Setchell, 2017). To give an example from our study, the chimpanzee community at Bulindi declined from 25 or more individuals in Period 1 to 19 individuals when research resumed in 2012, a minimum decrease of 24% in 4.5 years. The cause of this decline remains uncertain; however, at least three individuals were caught in large steel traps (used by some farmers to protect crops)



FIGURE 3 Two adult males of the Bulindi chimpanzee community seated in a coffee garden sharing a large cultivated jackfruit (*Artocarpus heterophyllus*) (Photo by Jacqueline Rohen)

during this interval and likely died (McLennan et al., 2012). All three confirmed deaths of independent chimpanzees since 2012 have been human-caused: two adults died after being injured by steel traps (Cibot, Le Roux, Rohen, & McLennan, 2019), whereas an adult female (with her infant) died in a vehicle collision (McLennan & Asimwe, 2016). A fourth individual, a wide-ranging adult male, was likely killed by villagers outside the community range. Thus, population dynamics of chimpanzees and other primates in fragmented matrix habitats might be driven primarily by human impacts, as also suggested for some other animals (e.g., large carnivores; Swanepoel et al., 2015; Vickers et al., 2015).

Where primates share habitats closely with people and eat crops habitually, residents may view them as a significant hindrance to livelihood security and economic growth (Dore, Eller, & Eller, 2018; McLennan & Hill, 2012; Paterson & Wallis, 2005). Long-term data are needed to establish whether potential benefits (e.g., energetic, reproductive) of foraging in agricultural matrix habitats outweigh fitness costs from human-driven mortality risk for chimpanzees and other adaptable primates (cf. Warren, Higham, MacLarnon & Ross, 2011). If not, such habitats may represent "ecological traps" for primates, as suggested for some other mammals (e.g., Northrup, Stenhouse, & Boyce, 2012; Simon & Fortin, 2019).

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ORCID

Matthew R. McLennan  <http://orcid.org/0000-0002-5925-1483>

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SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section.

APPENDIX A

TABLE A1 List of identified plant food items recorded in the diet of chimpanzees in Bulindi, Uganda, during studies conducted between 2007 and 2019^a

Plant Species	Family	Life form ^b	Part eaten ^c	First record in diet ^d
1. <i>Acacia</i> sp.	Fabaceae	T	Sd	3
2. <i>Acalypha</i> sp.	Euphorbiaceae	S	L [‡]	1 [§]
3. <i>Acanthus pubescens</i>	Acanthaceae	S	Pi ^{TV}	1
			W	3
4. <i>Aframomum angustifolium</i>	Zingiberaceae	H	Fr ^R	1
			Pi ^{TV}	1
5. <i>Aframomum verrucosum</i>	Zingiberaceae	H	Fr ^R	1
			Pi ^{TV}	1
6. <i>Albizia glaberrima</i>	Fabaceae	T	Pi ^{TB}	2
7. <i>Alchornea cordifolia</i>	Euphorbiaceae	S	Pi ^{TV}	2
8. <i>Allophylus africanus</i>	Sapindaceae	T	Fr ^R	1
9. <i>Allophylus ferrugineus</i>	Sapindaceae	S	Fr ^R	1
10. <i>Ampelocissus abyssinica</i>	Vitaceae	C	Fr ^R	1
11. <i>Ampelocissus africana</i>	Vitaceae	C	Fr ^R	1
12. <i>Aneilema nyasense</i>	Commelinaceae	H	L [‡]	1
			Pi ^{TV}	2 [§]
13. <i>Annona senegalensis</i>	Annonaceae	T	Fr ^R	1
14. <i>Antiaris toxicaria</i>	Moraceae	T	Fl	1
			Fr ^R	1
			L	1
			Pi ^{TV}	2
15. <i>Artocarpus heterophyllus</i> [†]	Moraceae	T	Fr ^{R, UR}	1
16. <i>Broussonetia papyrifera</i>	Moraceae	S	L	2
			Pi ^{TV}	3
17. <i>Caloncoba crepiniana</i>	Achariaceae	T	Fr ^R	1
18. <i>Canavalia</i> sp.	Fabaceae	S	Sd	1
19. <i>Canthium oligocarpum</i>	Rubiaceae	S	L	3 [§]
20. <i>Capparis erythrocarpus</i>	Capparaceae	S	Fr ^R	1
21. <i>Carica papaya</i> [†]	Caricaceae	T	Fr ^{R, UR}	1
22. <i>Celtis africana</i>	Cannabaceae	T	L	1 [§]
23. <i>Cissus</i> sp.	Vitaceae	C	Fr ^R	1

(Continues)

TABLE A1 (Continued)

Plant Species	Family	Life form ^b	Part eaten ^c	First record in diet ^d
24. <i>Citrus limon</i> [†]	Rutaceae	S	Fr ^{R, UR}	2
25. <i>Citrus sinensis</i> [†]	Rutaceae	S	Fr ^R	1
26. <i>Coccinia</i> sp.	Cucurbitaceae	C	Fr ^R	1
27. <i>Crassocephalum vitellinum</i>	Asteraceae	C	L ^R	2
28. <i>Crotalaria rogersii</i>	Fabaceae	H	L	1
29. <i>Croton macrostachyus</i>	Euphorbiaceae	T	B/c Pi ^{TB}	3 [§] 3 [§]
30. <i>Croton sylvaticus</i>	Euphorbiaceae	T	Fr ^R	1
31. <i>Culcasia falcifolia</i>	Araceae	C	Pi ^{TV}	2 [§]
32. <i>Cyperus papyrus</i>	Cyperaceae	H	Pi ^{TV}	1
33. <i>Dioscorea alata</i> [†]	Dioscoreaceae	H	L Pi ^{TV}	2 [§] 1
34. <i>Dioscorea odoratissima</i>	Dioscoreaceae	H	L	2
35. <i>Dovyalis macrocalyx</i>	Salicaceae	S	Fr ^R L	1 3
36. <i>Ekebergia capensis</i>	Meliaceae	T	Pi	2 [§]
37. <i>Entada abyssinica</i>	Fabaceae	T	L	1 [§]
38. <i>Entandrophragma</i> sp.	Meliaceae	T	B/c	2
39. <i>Eucalyptus</i> sp. [†]	Myrtaceae	T	B/c Pi ^{TB}	3 2
40. <i>Eureiandra</i> sp.	Cucurbitaceae	C	L [‡]	2
41. <i>Ficus asperifolia</i>	Moraceae	S	Fr (fig) ^{R, UR} L	1 2
42. <i>Ficus exasperata</i>	Moraceae	T	Fr (fig) ^{R, UR} L	1 2
43. <i>Ficus mucoso</i>	Moraceae	T	Fr (fig) ^{R, UR} L	1 2
44. <i>Ficus natalensis</i>	Moraceae	T	Fr (fig) ^R L	1 2
45. <i>Ficus ovata</i>	Moraceae	T	Fr (fig) ^R L Pi ^{TB}	2 3 2
46. <i>Ficus sansibarica</i>	Moraceae	T	Fr (fig) ^{R, UR} Pi ^{TB} Sp	2 2 2 [§]
47. <i>Ficus sur</i>	Moraceae	T	Fr (fig) ^{R, UR} L Sp	1 2 2 [§]
48. <i>Ficus thonningii</i>	Moraceae	T	Fr (fig) ^{R, UR} L	1 2
49. <i>Ficus vallis-choudae</i>	Moraceae	T	Fr (fig) ^{R, UR} L Pi ^{TB}	2 2 2

(Continues)

TABLE A1 (Continued)

Plant Species	Family	Life form ^b	Part eaten ^c	First record in diet ^d
50. <i>Ficus variifolia</i>	Moraceae	T	Fr (fig) ^R	1
			L	1
			Sp	1 ^s
51. <i>Flueggea virosa</i>	Phyllanthaceae	S	Fr ^R	3
52. <i>Glennia africana</i>	Sapindaceae	T	Pi ^{TB}	2 ^s
53. <i>Grewia mollis</i>	Malvaceae	S	Fr ^R	1
54. <i>Grewia pubescens</i>	Malvaceae	S	Fr ^R	1
55. <i>Harungana madagascariensis</i>	Guttiferae	T	Pi ^{TV}	2 ^s
56. <i>Hibiscus calyphyllus</i>	Malvaceae	S	Fl	2
57. <i>Hoslundia opposita</i>	Lamiaceae	S	Fl	3
			Fr ^R	3
58. <i>Illigera pentaphylla</i>	Hernandiaceae	C	L	2
59. <i>Khaya anthotheca</i>	Meliaceae	T	B/c	2
60. <i>Landolphia landolphioides</i>	Apocynaceae	C	Fr ^{R, UR}	1
61. <i>Lantana camara</i>	Verbenaceae	S	Fr ^R	1
			L [‡]	1
62. <i>Lantana trifolia</i>	Verbenaceae	S	Fr ^R	1
63. <i>Leea guineensis</i>	Vitaceae	S	Fr	1 ^s
64. <i>Macaranga schweinfurthii</i>	Euphorbiaceae	T	Fr	1
			Pi ^{TB}	2
65. <i>Macrosphyra longistyla</i>	Rubiaceae	S	L [‡]	2 ^s
66. <i>Maesopsis eminii</i>	Rhamnaceae	T	Fr ^R	1
67. <i>Mangifera indica</i> [†]	Anacardiaceae	T	Fr ^{R, UR}	1
68. <i>Marantochloa leucantha</i>	Marantaceae	H	Fr ^R	1
			L	3
			Pi ^{TV}	1
			R	2
69. <i>Markhamia lutea</i>	Bignoniaceae	T	Pi ^{TV}	2 ^s
70. <i>Merremia pterygocaulos</i>	Convolvulaceae	C	L	3
71. <i>Momordica calantha</i>	Cucurbitaceae	C	Fr ^{R, UR}	2
			L [‡]	3 ^s
72. <i>Monanthotaxis ferruginea</i>	Annonaceae	S	Fr ^R	1
73. <i>Morus mesozygia</i>	Moraceae	T	Fr ^R	1
			L	1
74. <i>Musa spp.</i> [†]	Musaceae	H	Fr ^{R, UR}	1
			Pi ^{TV}	1
75. <i>Neoboutonia melleri</i>	Euphorbiaceae	T	B/c	2 ^s
			Fr	3 ^s
76. <i>Neonotonia wightii</i>	Fabaceae	C	L	3
77. <i>Oncoba spinosa</i>	Salicaceae	T	Fr	1 ^s
78. <i>Palisota schweinfurthii</i>	Commelinaceae	H	Pi ^{TV}	1
79. <i>Parkia filicoidea</i>	Fabaceae	T	Fr ^R	1
			L	1
			Sd	1

(Continues)

TABLE A1 (Continued)

Plant Species	Family	Life form ^b	Part eaten ^c	First record in diet ^d
80. <i>Passiflora</i> spp. [†]	Passifloraceae	C	Fr ^R	1
81. <i>Pennisetum purpureum</i>	Poaceae	G	Pi ^{TV}	1
82. <i>Peponium vogelii</i>	Cucurbitaceae	C	Fr ^R	2
83. <i>Phaseolus vulgaris</i> [†]	Fabaceae	C	Fr ^{UR}	2
84. <i>Phoenix reclinata</i>	Arecaceae	T	Fr ^{R, UR}	1
			Pi ^{TV}	2
			Sd	2
85. <i>Piper guineense</i>	Piperaceae	C	L	2
86. <i>Piper umbellatum</i>	Piperaceae	S	Pi ^{TV}	2
87. <i>Piptadeniastrum africanum</i>	Fabaceae	T	Pi ^{TB}	3
88. <i>Platyserium angolense</i>	Polypodiaceae	E	L	3
89. <i>Pristimera graciliflora</i>	Celastraceae	S	Pi ^{TV}	2 [§]
90. <i>Pseudarthria hookeri</i>	Fabaceae	H	L [†]	1
91. <i>Pseudospondias microcarpa</i>	Anacardiaceae	T	Fr ^{R, UR}	1
			L	1
			Pi ^{TB}	2
92. <i>Psidium guajava</i> [†]	Myrtaceae	T	Fr ^{R, UR}	1
93. <i>Psychotria peduncularis</i>	Rubiaceae	S	Fr	1 [§]
94. <i>Rothmannia whitfieldii</i>	Rubiaceae	S	Fr	1
95. <i>Rourea thomsonii</i>	Connaraceae	S	Fl	3
			L	3
96. <i>Rubus pinnatus</i>	Rosaceae	S	Fr ^R	1
97. <i>Saccharum officinarum</i> [†]	Poaceae	G	Pi ^{TV}	1
98. <i>Setaria megaphylla</i>	Poaceae	G	Pi ^{TV}	2 [§]
99. <i>Sida rhombifolia</i>	Malvaceae	S	L	1 [§]
100. <i>Solanum betaceum</i> [†]	Solanaceae	S	Fr ^R	1
101. <i>Sonchus asper</i>	Asteraceae	H	L	3
102. <i>Sorghum arundinaceum</i>	Poaceae	G	Pi ^{TV}	2
103. <i>Spathodea campanulata</i>	Bignoniaceae	T	Fl	3
104. <i>Sterculia dawei</i>	Malvaceae	T	B/c	2
			Fl	2
			Fr ^{UR}	2
			L	1
105. <i>Syzygium guineense</i>	Myrtaceae	T	Fr ^R	3
106. <i>Theobroma cacao</i> [†]	Malvaceae	T	Fr ^{R, UR}	1
107. <i>Toddalia asiatica</i>	Rutaceae	S	Fr ^R	1
108. <i>Trema orientalis</i>	Cannabaceae	T	Pi ^{TB}	3 [§]
109. <i>Trichilia dregeana</i>	Meliaceae	T	L	1
			Pi ^{TB}	2
110. <i>Trilepisium madagascariensis</i>	Moraceae	T	L	2
111. <i>Tylophora</i> sp.	Apocynaceae	C	L	3
112. <i>Urera trinervis</i>	Urticaceae	C	L	3
			Pi ^{TV}	2
113. <i>Uvaria angolensis</i>	Annonaceae	C	Fr ^R	1
114. <i>Vangueria madagascariensis</i>	Rubiaceae	T	Fr ^R	1

(Continues)

TABLE A1 (Continued)

Plant Species	Family	Life form ^b	Part eaten ^c	First record in diet ^d
115. <i>Vernonia amygdalina</i>	Asteraceae	S	Pi ^{TV}	2 [§]
116. <i>Vigna vexillata</i>	Fabaceae	C	Fl	3 [§]
117. <i>Vitex doniana</i>	Lamiaceae	T	Fr ^R	1
118. <i>Zanha golungensis</i>	Sapindaceae	T	Fr ^R	1
			L	2
119. <i>Zea mays</i> [†]	Poaceae	G	Pi ^{TV}	2

^aPlant foods were recorded in the diet by direct observation, fecal analysis, and/or feeding trace evidence; the chimpanzees were habituated by 2015, after which fecal analysis was discontinued and diet was recorded mainly via direct observation.

^bLife form: C, climber (liane or vine); E, epiphyte; G, grass; H, herb; S, shrub; T, tree.

^cPart eaten ($n = 169$ food items): B/c, bark or cambium (comprising 3.6% of food items); Fl, flower or inflorescence (4.1% items); Fr, fruit (38.5% items; ripeness of fruits and figs eaten is indicated, where determined: R, ripe; UR, unripe); L, leaf (26.0% items; leaf foods ordinarily comprise young leaves or shoots; [†]mature leaves may be eaten in the context of whole leaf-swallowing, that is, presumed self-medication; see McLennan, Hasegawa et al., 2017); Pi, pith/stem (22.5% items; pith from terrestrial vegetation [TV] including herbs, shrubs, and tree saplings are distinguished from pith from terminal tree branches [TB], where determined); R, root (0.6% items); Sd, seed (2.4% items); Sp, sap (1.8% items); W, wood (0.6% items).

^dIndicates the first record of an item in the diet of chimpanzees in Bulindi, divided into three research phases: 1 = January 2007–January 2008 (Period 1); 2 = September 2012–December 2015 (includes Period 2); 3 = January 2016–June 2019 (subsequent to the periods considered in this paper). Note that a food item newly recorded in phases 2 or 3 does not imply a “new” food for the chimpanzees, only that the item was not previously confirmed eaten. Dietary data were not collected continuously in phases 2 and 3.

[§]Denotes an item recorded eaten once only (i.e., in a single feeding observation, fecal sample, or feeding trace).

[†]Denotes a cultivated crop/exotic; for common names of crops see Table 3.