Wild chimpanzees show group differences in selection of agricultural crops

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The ability of wild animals to respond flexibly to anthropogenic environmental changes, including agriculture, is critical to survival in human-impacted habitats. Understanding use of human foods by wildlife can shed light on the acquisition of novel feeding habits and how animals respond to human-driven land-use changes. Little attention has focused on within-species variation in use of human foods or its causes. We examined crop-feeding in two groups of wild chimpanzees – a specialist frugivore – with differing histories of exposure to agriculture. Both groups exploited a variety of crops, with more accessible crops consumed most frequently. However, crop selection by chimpanzees with long-term exposure to agriculture was more omnivorous (i.e., less fruit-biased) compared to those with more recent exposure, which ignored most non-fruit crops. Our results suggest chimpanzees show increased foraging adaptations to cultivated landscapes over time; however, local feeding traditions may also contribute to group differences in crop-feeding in this species. Understanding the dynamic responses of wildlife to agriculture can help predict current and future adaptability of species to fast-changing anthropogenic landscapes.

Extensive transformation of natural habitats to alternative land-uses by people means that wild animals must adapt to rapidly changing environmental conditions, migrate, or perish[1]. While land-use changes including cultivation, plantation forestry, ranching and urbanisation invariably erode wild food supplies, they provide wildlife with opportunities to feed on novel foods such as agricultural crops, introduced exotics, garbage and livestock[2–5]. Understanding use of human food sources by wild animals is of considerable interest since it can shed light on the acquisition of novel feeding habits and the process by which species adjust their behaviour in response to rapidly changing environments. To date, little attention has focused on potential variation among conspecific populations in use of human foods or its causes. In this study we compared crop-feeding in two allopatric populations of chimpanzees (*Pan troglodytes*) – an endangered mammal, threatened by habitat loss – to better understand how human foods are assimilated into animal diets under conditions of dynamic land-use change.

Some wild animals never or rarely exploit human foods and fare badly in human-modified environments. However, populations of certain species are able to prosper in association with people and may rely on human activities for a substantial portion of their diet (e.g., some species of macaque monkey, *Macaca*[6]). The extent to which wildlife utilise anthropogenic environments including human food sources will depend on species-specific traits, as well as local people's attitudes toward the species. In particular, species exhibiting high behavioral plasticity and dietary flexibility should cope better with human habitat alterations than ecological specialists[1,7]. In medium- to large-bodied mammals, this is reflected in the predominance of omnivorous, generalist feeders among species that commonly exploit human foods, for example African elephants *Loxodonta africana*[8], black bears *Ursus americanus*[9], and wild boars *Sus scrofa*[10], as well as certain primates including olive baboon *Papio anubis*[11] and rhesus macaque *Macaca mulatta*[6].

Chimpanzees do not confirm wholly to this pattern. While the natural diet of this great ape is broadly omnivorous, comprising diverse plant and animal foods, chimpanzees are not generalist feeders. They preferentially seek out ripe fleshy fruits, which are often seasonal and patchily distributed, and exhibit flexible socio-behavioural adaptations (high fission–fusion dynamics) which enable them to pursue a fruit-dominated diet even when fruit is scarce[12]. Consequently, chimpanzees are usually considered ripe fruit specialists[13,14]. This more selective foraging strategy sets chimpanzees apart from many other mammals that exploit agricultural environments.

Nevertheless, like some other great apes (e.g., orang-utans *Pongo* spp.), chimpanzees exhibit considerable behavioural plasticity, including innovative behaviours and 'cultural' variation[15,16]. This suggests they may have an ability to respond flexibly to anthropogenic environmental changes, including agriculture, if protected from persecution. Innovative feeding behaviours are an important part of behavioural flexibility[17], and potentially critical to the survival of species inhabiting human-impacted habitats. Experiments in the wild and captivity showed that chimpanzees exhibit initial neophobic responses towards novel foods[18,19]. However, other evidence suggests wild chimpanzees have a propensity to experiment with exotic foods introduced into their habitats including agricultural crops[20], but that their assimilation into the diet is a gradual process[21].

Cultivated foods tend to be highly palatable, easily digestible, and spatially concentrated in fields or plantations, offering foraging advantages over many natural foods[22,23]. A review of crops eaten by chimpanzees across their geographical range revealed they feed on an unexpectedly diverse array of crops and crop parts. Even so, fleshy sugary fruits dominate the list of crops eaten, consistent with the selective foraging strategy of a frugivore[24]. Chimpanzees ignore some widely cultivated non-fruit crops (e.g., most vegetables)[24] that are readily exploited by other crop-raiding mammals, including sympatric primates (e.g., olive baboon, black and white colobus monkey *Colobus guereza* and tantalus monkey *Chlorocebus tantalus* in Uganda[11,25]). Chimpanzees also show potential local differences in use of particular crops[24]. Failure to utilise nutritionally-dense, energy rich crops might imply their dietary response is overly conservative for long-term survival in expanding agricultural environments (i.e., insufficiently flexible). Whether chimpanzees reduce their feeding selectivity to more fully exploit agricultural landscapes over time is unknown. Additionally, if purported local differences in crop selection exist, what factors might contribute to this variation?

Here we examine crop-feeding by two populations (hereafter 'communities') of wild chimpanzees inhabiting small forest fragments amid agricultural systems. Eastern chimpanzees (*P. t. schweinfurthii*) at Bulindi, Uganda, have experienced recent rapid habitat alteration, with extensive logging and near-total clearance of forest for agriculture since c.2000 to the present[26]. Persistent crop-raiding and use of farmland by chimpanzees is considered "recent" by villagers[27]. Western chimpanzees (*P. t. verus*) at Bossou, Guinea, have a longer history of coexistence with farmers for whom the apes are a totem, and have exploited agricultural crops for generations[28,29]. While considerable deforestation has occurred at Bossou, remaining forest is sacred in local mythology and has not recently experienced very high rates of clearance and logging as witnessed at Bulindi[29]. Thus, Bulindi chimpanzees have a shorter history of major habitat disturbance and exposure to agriculture compared to those in Bossou. Our aim here is to determine to what extent chimpanzees exhibit selectivity in crop-feeding and examine potential between-site differences in crop selection. We predicted that:

1. As selective feeders chimpanzees will target particular crops preferentially. Therefore consumption of a crop will not be strongly related to its accessibility ('accessibility' is a composite measure of each crop's availability incorporating several environmental factors; see Methods).
2. Chimpanzees will show strong selectivity for fruit crops over non-fruit crops with accessibility controlled for.
3. A crop selected by chimpanzees at one site will be selected by chimpanzees at the other, if accessible. However, if chimpanzees can adapt their foraging behaviour over time to exploit agricultural landscapes more fully, crop-feeding by Bossou chimpanzees (with longer exposure to crops) will be less selective towards fruits compared to Bulindi (more recent exposure).

Results

Crop-feeding by chimpanzees was recorded at a similar overall frequency at both sites over 12 months: on 120 days at Bulindi (maximum number of different crop foods consumed daily = 6) and 134 days at Bossou (maximum = 7). In total 20 crop foods from 18 different crops were consumed at the 2 sites; 12 were fruits while 8 were non-fruits (Figure 1; Supplementary Table).

Crop accessibility was a significant predictor of consumption by chimpanzees at both sites (Table 1), accounting for 30% of variation in consumption of individual crops at Bulindi ($F_{1,18} = 7.52$, P = 0.013) and 68% at Bossou ($F_{1,18} = 38.06$, P < 0.001). Thus, crop accessibility had a stronger effect on consumption at Bossou. Introducing crop-type (i.e., fruit and non-fruit) improved both models significantly (indicated by the change in R^2 in Table 1), explaining an additional 18% of variation in crop consumption at Bulindi ($F_{2,17} = 7.57$, P = 0.004) and a further 10% at Bossou ($F_{2,17} = 29.90$, P < 0.001). Chimpanzees at both sites consumed fruit crops significantly more frequently than non-fruit crops when the effects of accessibility were held constant.

The ranked distribution of crop accessibility scores did not differ between sites (U = 179.5, z = −0.565, n = 20, p = 0.58), suggesting that crop foods were overall similarly accessible to both communities. This result held when fruit and non-fruit foods were considered separately (fruit: U = 55.0, z = −1.000, n = 12, p = 0.33; non-fruit: U = 27.0, z = −0.546, n = 8, p = 0.59). Nevertheless, between-community differences in consumption of individual crops were apparent: 13 of 20 crop foods were consumed at 1 of the 2 sites only (Supplementary Table). In only 5 cases was the crop inaccessible within the core area of the community that did not consume it (Figure 1). When considered in relation to crop-type and accessibil-
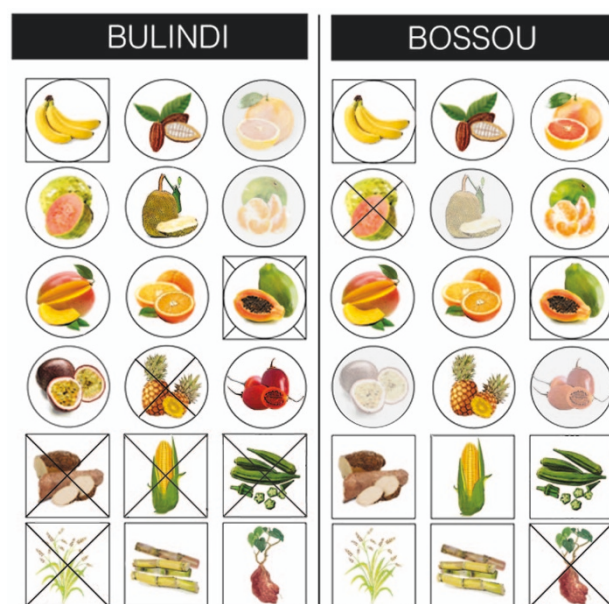

Figure 1 | Comparison of crop foods consumed by chimpanzees at Bulindi and Bossou. Crops arranged from top-left corner: banana, cocoa, grapefruit, guava, jackfruit, mandarin, mango, orange, papaya, passion fruit, pineapple, tamarillo, cassava, maize, okra, rice, sugarcane, yam. Circular icons indicate fruits while square icons indicate non-fruits (see Methods). Both of these 'crop types' may be consumed in the case of banana (fruit and pith) and papaya (fruit and leaf). Grey-shaded icons denote a crop not accessible within the core area of the respective chimpanzee community. Crossed-through icons denote an accessible crop which was not consumed by the chimpanzee community during the study. Bulindi chimpanzees consumed 12 crop foods (including 9 fruits and 3 non-fruits) while Bossou chimpanzees consumed 15 (8 fruits and 7 non-fruits) (artwork by Stacey Hockings).

Table 1 | Summary of hierarchical regression analysis of the effect of crop accessibility and crop-type (fruit and non-fruit) on chimpanzees' consumption of 20 agricultural crop foods at Bulindi and Bossou

Site	Predictor variable	b	SE	95% CI	β	t	P	R^2	Δ R^2
Bulindi	Step 1							.30	–
	Accessibility	0.922	0.336	0.216–1.629	.543	2.742	0.013		
	Step 2							.47	.18
	Accessibility	1.077	0.307	0.430–1.724	.634	3.512	0.003		
	Crop-type	2.154	0.905	0.246–4.062	.430	2.381	0.029		
Bossou	Step 1							.68	–
	Accessibility	7.583	1.229	5.000–10.165	.824	6.169	<0.001		
	Step 2							.78	.10
	Accessibility	9.289	1.218	6.720–11.858	1.009	7.629	<0.001		
	Crop-type	10.541	3.808	2.506–18.575	.366	2.768	0.013		

For each predictor the following model parameters are shown: unstandardised b-coefficients (b) with associated standard error (SE) and 95% confidence intervals (CI), standardised Beta coefficients (β), t tests and their significance. Also reported are R^2 values for each step of the models and the change in R^2 (Δ R^2) from Step 1 to Step 2. In both models a significant (positive) increase in frequency of consumption associated with a change in crop-type reflects the change from non-fruit to fruit crops.

ity, the following patterns were evident: (i) only fruit crops that were inaccessible or, in one case at each site, had 'low' accessibility scores were not eaten. In contrast, all non-fruit crops that were not consumed at one site were accessible to both communities (Figure 2); (ii) while a similar number of fruit crops were not eaten at both sites, 5 non-fruit crop foods were not consumed at Bulindi compared to just 1 at Bossou. Further, 4 of those that were not consumed at Bulindi had 'high' accessibility scores (cassava, maize, papaya leaf, rice) (Figure 2).

Discussion

Wild chimpanzees at Bulindi and Bossou inhabit forest–agricultural mosaics and both communities exploit a variety of human foods, including fruit and non-fruit crops. Crop feeding is a habitual foraging activity at both sites. For example, crops accounted for 14% of total feeding time at Bossou during this study (monthly range: 3.6–26.3%)[30]. Crop accessibility was a primary determinant of consumption, with more accessible crops eaten most frequently at both sites. This was against prediction because chimpanzees are not considered generalist or opportunist feeders like many crop-raiding mammals; consequently, we expected them to exhibit greater selectivity. However, some crops were ignored by both communities (e.g., most vegetables[24]) and these were not considered in our analysis. Furthermore, with accessibility controlled for, both communities consumed fruit crop foods more often than non-fruit crop foods, in agreement with our prediction.

For those crops consumed by at least one community, our results revealed a marked site difference in selection. The relationship between crop accessibility and consumption was stronger at Bossou, where chimpanzees have a longer history of crop-feeding. Both communities consumed most fruit crops, with cases of non-consumption attributable to lack of access or else low accessibility (and therefore limited opportunities to encounter the crop). However, only Bulindi chimpanzees ignored highly accessible non-fruit crops including several widely cultivated staple foods (e.g., maize, cassava and rice). At Bossou, chimpanzees fed on a greater diversity of non-fruit crops. They exploited maize and rice crops frequently when seasonally available (and irrespective of wild food availability)[30], and ate cassava year-round[31] (Figure 3). Thus, in the case of non-fruits (but not fruits), our prediction that a crop selected at one site would also be selected at the other was not supported.

The lack of evidence for use of these non-fruit crops at Bulindi was not attributable to a greater reliance on feeding trace evidence compared to direct observation (see Methods). Crop-feeding traces were recorded more readily than many wild (forest) foods, owing to the comparative ease of locating terrestrial feeding sites in croplands when tracking chimpanzee foraging routes among forest fragments. Notably, feeding traces of two non-fruit crops – sugarcane and banana pith – were recorded frequently[32]. Our findings that Bulindi chimpanzees ignored most other non-fruit crops strongly accord with local farmers' reports of crop losses to wildlife. A survey of 134 residents made concomitantly with this study found that
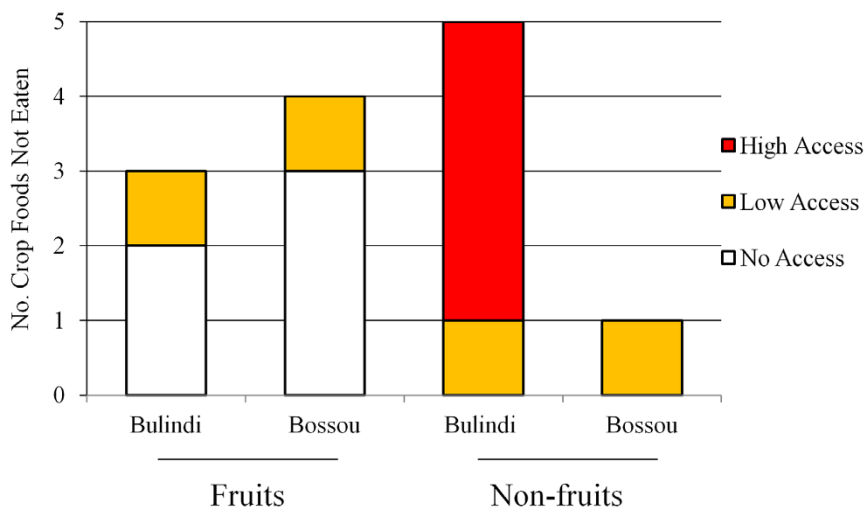

Figure 2 | Number and accessibility of crop foods that were *not* consumed by chimpanzees of the two communities: Bulindi (n = 8), Bossou (n = 5). In all cases the crop was consumed by chimpanzees of the other community. Accessibility of a crop within the chimpanzees' core area was classed as 'high', 'low' or 'not accessible' (see Methods). Fruit and non-fruit crop foods are displayed separately.
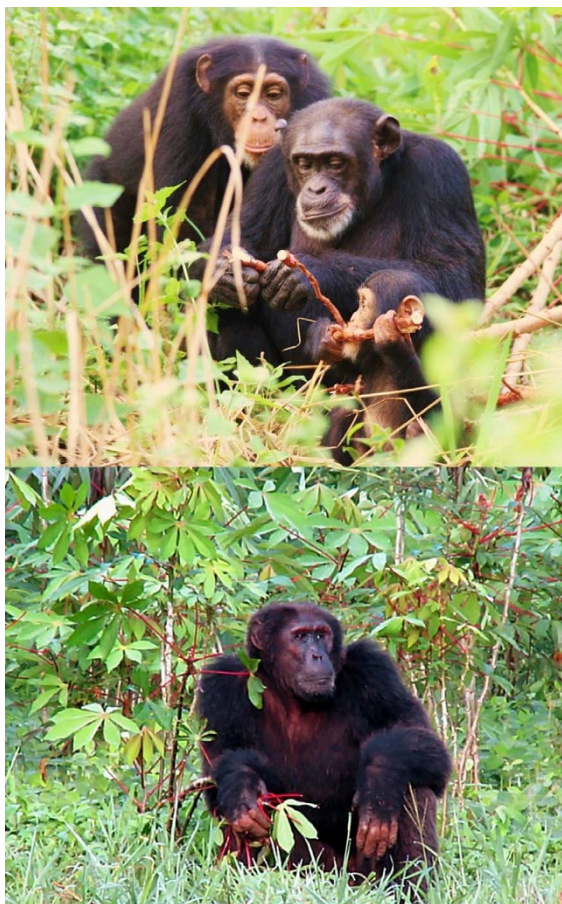
Figure 3 | Cassava tuber is highly accessible to chimpanzees at both sites but is only eaten at Bossou; (a) *Upper figure.* A juvenile chimpanzee watches closely as an adult female, with her infant, processes and feeds on cassava tubers at Bossou, Guinea (photo by Etsuko Nogami); (b) *Lower figure.* An adult male chimpanzee in a cassava field at Bulindi, Uganda. He is holding cassava leaves following a social display, but chimpanzees at this site have not been recorded to feed on any part of the plant (photo by Matthew McLennan).

chimpanzee damage to sugarcane and fruit crops was reported routinely by local households[27]. Conversely, chimpanzees were widely considered less destructive than other crop-raiding wildlife (principally other crop-raiding primates) precisely *because* they did not eat staple food crops including maize and cassava[27].

Crop varieties vary regionally in Africa, and crop growth, development and yield are impacted by climate. Consequently, crop varieties grown at Bulindi and Bossou may show subtle variation. At both sites maize and cassava are important human staple foods, making it unlikely that critical differences in nutritional content exist that explain why chimpanzees ate them at Bossou but not at Bulindi. Moreover, maize cob is eaten by chimpanzees elsewhere in Uganda[24] including by some chimpanzee communities within 20 km of Bulindi (M. McCarthy, pers. comm. 2014). Cassava cultivated at both sites is of the 'sweet' variety that can be eaten by humans uncooked (i.e., it does not contain toxic levels of cyanogenic glucosides)[31], and cassava is targeted by other crop-raiding primates in Bulindi. In the case of rice, we cannot exclude potential nutritional differences since rice grown within the chimpanzees' core area at Bossou is mostly paddy while at Bulindi farmers mostly cultivate upland varieties. Even so, olive baboons in Bulindi consume rice pith. Recently, Hayakawa *et al.*[33] reported genetic diversity of bitter taste receptors among chimpanzee subspecies. However, this unlikely explains site differences since these crops are exploited by chimpan-

zees in both East and West Africa[24]. We cannot presently assess whether optimal foraging models account for differences since nutritional and more fine-tuned spatial–temporal information for all accessible wild and cultivated foods within the home ranges of both communities is lacking. Thus, while we consider it unlikely, highly accessible non-fruit crops might be ignored at Bulindi if other more 'profitable' foods (i.e., providing a higher net energy return[34]) – wild or cultivated – are more accessible than at Bossou.

Wild animal diets can vary annually and supra-annually, including in chimpanzees[14]. This raises the possibility that crops not eaten in this 12-month study were in fact consumed outside the study period (i.e., they were already part of the chimpanzees' dietary repertoires). Two lines of evidence make this improbable. First, as discussed above, by strong consensus Bulindi farmers claimed chimpanzees did not eat staple food crops[27]. Second, more recent research at Bulindi (2012–present) similarly found no evidence of chimpanzees eating the non-fruit crops discussed here, with one exception: feeding traces reveal they occasionally consume the pith (but not the cob) of immature maize stalks. This most likely represents a recent change in feeding behaviour and not one that was simply missed in the present study: since 2012 farmers have frequently commented that, "now the chimpanzees have *started* eating our maize" (M.M., unpublished data).

Novel food items that are comparable to existing foods (i.e., in shape, odour and colour, and requiring similar processing) are more likely to be recognised as edible and therefore integrated into animal diets quicker than unfamiliar foods. Chimpanzees probably recognise most fruit crops as edible from ripeness cues. But chimpanzees might not have parallels in their natural diet for non-fruit crops such as maize cob and cassava tuber, which may explain why apes at Bulindi failed to exploit them. Additionally, the consumed part of non-fruit crops is more often less visible or embedded (e.g., tubers) compared to most fruits – a further reason why chimpanzees may be slow to recognise such crops as food.

Our current data do not address whether Bulindi and Bossou chimpanzees *need* to exploit agricultural crops for survival, though this possibility seems more likely at Bulindi given the extent and speed of recent habitat conversion there[26]. In such circumstances, once a crop food is identified as 'profitable', its assimilation into the diet is expected to be faster than in environments where the natural food supply is not being eroded (Figure 4) (cf. the gradual acquisition of abandoned fruit cultivars into the chimpanzee diet at Mahale, Tanzania, following relocation of villagers from the National Park[20,21]). The process by which crops are assimilated into chimpanzee diets at the community-level remains unstudied. However, considering their capacity to learn from others[15,35], we anticipate that social learning plays a role in the incorporation of novel human food sources into chimpanzee diets, as has been demonstrated in some other species (e.g., African elephants[36]; black bears[37]; bottlenose dolphins *Tursiops aduncus*[38]) (see also Figure 3).

Divergent feeding preferences exist among populations of the same species, for example killer whales *Orcinus orca*[39] and orangutans *Pongo pygmaeus*[40]. In chimpanzees marked dietary differences can exist among adjacent or nearby communities[14,41], attributable in many instances to local variation in flora[26,42]. Nevertheless, differences are not always explained by environmental factors and might instead reflect local feeding traditions or 'cultures'[41,43,44].

Crop-feeding differences between Bulindi and Bossou thus might reflect feeding traditions maintained over generations. In particular, the failure of Bulindi chimpanzees to exploit certain crops might reflect their 'cultural ignorance' of these food sources[45]. However, agricultural expansion at the expense of natural habitat is expected to promote feeding experimentation and innovation in flexible species (Figure 4). We suggest that greater omnivorous (i.e., less fruit-biased) crop selection by chimpanzees at Bossou compared to Bulindi during this study is likely related to their longer history of
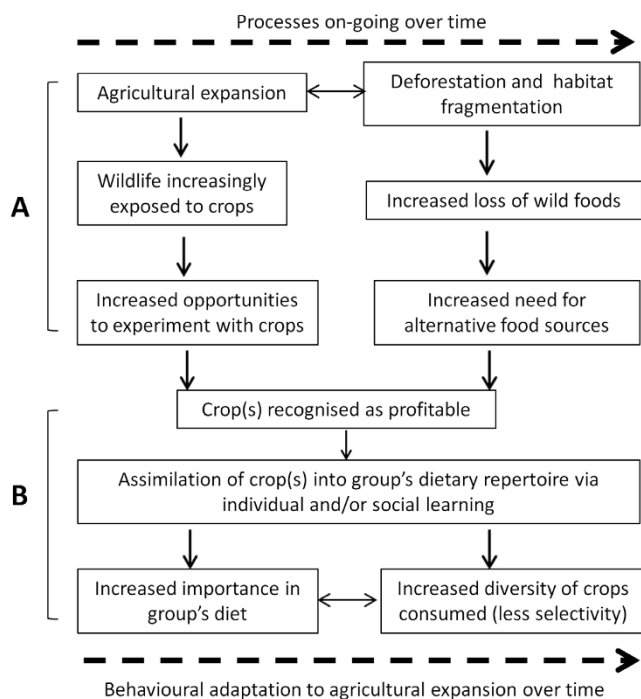
Figure 4 | Flowchart of the process by which agricultural crops are assimilated into wild animal diets following agricultural expansion into natural habitats. The ability of a species to move from A (increased exposure to crops) to B (assimilation into the diet and diversification of crops eaten) is determined by species traits, e.g., behavioural and ecological flexibility[1]. Variation among sites in the relative speed and extent of processes produces dynamic feeding patterns among conspecific groups.

exposure to farming and use of agricultural land. Thus we consider it probable that Bulindi chimpanzees, with less exposure time, have yet to recognise the profitability of some non-fruit crops. While this implies that all palatable crops will eventually be exploited given enough time, Bossou chimpanzees continue to ignore some accessible and palatable foods, for example avocado fruits. Thus, we cannot currently exclude feeding traditions (or 'cultural ignorance') as a potential contributor to divergent crop-feeding patterns in chimpanzees.

To survive in human-dominated landscapes animals must take advantage of resources available, including human foods, while minimising risks associated with costly encounters with people and other indirect dangers (e.g., crop protection techniques). Our findings provide support for the prediction that chimpanzees exhibit increased foraging adaptations to cultivated environments over time by exploiting a greater diversity of crops (Figure 4). While indicative of behavioral and ecological adaptability in the face of anthropogenic habitat alteration, chimpanzees' capacity to exploit agricultural foods might lead them into an 'evolutionary trap'[46]. Use of farmland and human settlements increases exposure to potentially deleterious human and livestock pathogens[47,48]. Moreover, crop-feeding by great apes and other wildlife may be associated with growing human–wildlife 'conflicts'[49,50]. Crop losses can instigate retributive killing and use of lethal crop protection methods, potentially leading to local extirpation of crop-raiding animals[51,52]. In such circumstances, 'adaptive' exploitation of human foods by threatened wildlife including chimpanzees may be regarded as maladaptive if it reduces fitness[37,38,46,53].

As conversion of natural habitats for agriculture continues to occur throughout the World's most biodiverse regions[54–56], exposure to crops and landscapes dominated by human cultivation are contemporary events for many wildlife populations. In contrast to more stable habitats, where exposure to novel wild foods is rare, rapidly changing human-dominated environments can generate dynamic feeding patterns among animals, with complex interactions between site-specific anthropogenic and environmental factors and species characteristics. Understanding the dynamic nature of wildlife responses to agricultural exposure, at the species-level and more broadly, offers a useful framework for predicting the current and future adaptability of animal populations to fast-changing anthropogenic habitats, and will aid more effective conservation management[24].

Methods

Study sites. Chimpanzees at Bulindi, Uganda (1°28′N, 31°28′E) have been studied since 2006[57] whereas research at Bossou, Guinea (7°39′N, 8°29′W) has been on-going since 1976[29]. At both sites smallholder farmers practise subsistence farming with some cash-cropping, and there is substantial overlap in crops grown. Common food crops include maize, cassava, potato, banana, rice, and ground nuts[25,27,29,30], which have been cultivated for decades at both sites. In Bulindi rice has been more widely cultivated during the last decade than previously. At both sites the area given over to cultivation of a particular crop varies among crops and households considerably. However, most crops are typically grown in fields < 10,000 m² with staple food crops like cassava and maize tending to be grown in largest areas[25,31]. Domestic fruits (e.g., papaya) mostly occur as individual trees.

The chimpanzee communities numbered >25 individuals at Bulindi and 12–14 at Bossou during study periods considered here. The habitually-used portion of the home range ('core area') was similar at both sites (ca. 5–6 km²), comprising small forest patches amid abandoned and cultivated fields adjacent to villages[30,57]. At both sites forest fruit availability fluctuated seasonally, and chimpanzees of both communities increased consumption of cultivated fruits during periods of forest fruit scarcity[30,32]. However, for some seasonal crops, consumption by chimpanzees was closely linked to availability (e.g., mango at both sites; maize at Bossou)[30,32]. At Bulindi other medium-bodied wild mammals feed on humans foods including primates (*Papio anubis*, *Chlorocebus tantalus*, and *Colobus guereza*), porcupine *Hystrix cristata* and wild pig *Potamochoerus* sp.[27]. Overt competition for agricultural crops has not been observed between chimpanzees and such species. At Bossou, most other medium-to-large mammals have been hunted out of local forests including other diurnal primates[58]. Domestic animals (e.g., cow, goat, pig) damage crops at both sites.

Data collection. Crop consumption by chimpanzees was examined in each calendar month over 12 months (Bulindi: January–December 2007; Bossou: between May 2004–December 2005). We obtained a simple measure of the frequency of consumption of individual crops (see Data Analysis). At Bossou crop-feeding was recorded using all-occurrences sampling during follows of chimpanzees (see Hockings et al.[30]). At Bulindi, chimpanzees were often observable but were not sufficiently habituated to systematic observation methods. Data on crop-feeding were therefore collected by examining fresh (same day) feeding traces during daily tracking, supplemented by frequent opportunistic observations of feeding behaviour[32,57]. While faecal analysis was used previously to quantify diet at Bulindi, non-fruit foods (e.g., pith, leaves) are not readily identifiable to species in faeces[32]. Therefore we did not use faecal data in the present analysis. In contrast, feeding traces are not subject to a fruit bias. Crop feeding traces were recorded by following fresh chimpanzee trails (i.e., signs of passage through grass or standing crops, typically with knuckle and foot prints and/or faeces) to and from feeding sites within or at edges of fields, often after chimpanzees were observed on farmland. Feeding traces were also encountered more opportunistically, particularly after chimpanzees carried crop foods back from fields or homes to consume at forest edges. Feeding traces could ordinarily be assigned readily to chimpanzees on the basis of species-typical manner of processing, bite size, and/or associated sign (e.g., faeces). However, if there was any doubt that animals other than chimpanzees were responsible for traces, they were not recorded.

We only considered crops that are planted by people and do not occur naturally at either site, though several which we do consider also occur as naturalised specimens. Thus, we excluded oil-palm (*Elaeis guineensis*) and raphia-palm (*Raphia gracilis*) at Bossou because these predominantly grow wild, while also being cultivated or tended to by people. We also excluded crops for which only a single observation of consumption by one individual was recorded (e.g., avocado leaf and okra seed pod at Bossou). We did not consider crops ignored by both chimpanzee communities (e.g., potato; see Hockings & McLennan[24]). For other crops, we considered all feeding records regardless of location or context, i.e., whether consumed via crop-raiding (broadly defined as 'taking food that local people view as belonging to them'[24]) or from abandoned or naturalised sources. We assumed a crop cultivated at both sites had comparable palatability and any differences in nutritional content were minimal (see Discussion).

Data analysis. For each community we totalled the number of days in which individual crop foods were recorded consumed (whether through observation or feeding traces). We retained only one feeding record per crop per day. Thus 'consumption' refers to the number of days a particular crop food was recorded eaten at either site over 12 months; it does not indicate feeding time, quantity ingested or

number of individuals that fed on it. We categorised crop foods into two 'crop-types': fleshy fruits containing soft sugary pulp (hereafter 'fruit') and non-fruits, which include plant parts such as pith (or stem), leaf and tuber, as well as maize cob which – while botanically fruit – lacks soft fleshy pulp. Chimpanzees may consume food of both crop-types from the same cultivar (e.g. banana fruit and pith)[24].

Accessibility of particular crops to chimpanzees is determined by human factors (i.e., guarding, crop protection) as well as environmental ones, and varies among crops and individual farms. Farmers at both sites occasionally threaten 'raiding' chimpanzees (e.g., by shouting, throwing stones or chasing after them). In Bulindi steel 'man-traps' are sometimes placed at field or forest edges to deter crop-raiding wildlife[52]. But at both sites farmer guarding and crop protection is sporadic and does not prevent chimpanzees from accessing target crops from localities across their home ranges (M.M. and K.H., unpublished data). Therefore we did not consider human factors. To investigate how accessibility affects consumption, for each site we calculated an accessibility index for all crops consumed at either site by summing scores for five binary environmental indicators:

Presence within chimpanzee core area: 1 = present, 0 = absent;

Occurrence: 1 = common, 0 = uncommon (grown by most or a minority of local farmers, respectively);

Cultivated area: 1 = large (typically grown in plantations, orchards or large fields, e.g., staple food crops), 0 = small (typically grown in small fields or scattered groves, e.g., minor food crops and domestic fruit trees);

Location: 1 = available both inside (whether from a cultivated, abandoned or naturalised source) and outside forest, 0 = available exclusively outside forest (crop fields and village);

Seasonality: 1 = available in most or all months of year, 0 = available during discrete fruiting, growing or harvesting season.

Accessibility scores thus ranged between 0–5. We considered scores of 3–5 indicative of 'high accessibility' and scores of 1–2 indicative of 'low accessibility'; a score of 0 meant a particular crop was 'inaccessible' within the core area of the community under consideration.

For example, the following accessibility index was calculated for cassava at Bossou[31]. Cassava was present within the chimpanzees core area (score = 1); it was cultivated by the majority of farmers (score = 1), typically in large fields (score = 1) both within and outside forest (score = 1), and was available year-round (score = 1). Thus, cassava at Bossou received a score of 5 and was considered highly accessible.

Statistics. All analyses were carried out using SPSS version 19.0. We performed a multiple regression analysis to evaluate the predictive relationship between accessibility and crop-type (independent variables) on crop consumption at each site separately. We did not model the effects of site on consumption because of the different methods used to record consumption. Crop-type was coded as a binary dummy variable (non-fruit = 0; fruit = 1). While accessibility was measured on an ordinal scale with six levels, we treated it as numerical because its underlying scale is continuous (i.e., crops occur along a continuum of accessibility), assuming that 'distances' between adjacent levels are approximately equal[59]. Because we wished to examine the effect of crop-type on consumption independently of accessibility, we employed a hierarchical regression model with accessibility entered in Step 1 and crop-type entered in Step 2. We determined test assumptions were met via diagnostics computed in SPSS[60]. Specifically, the variance inflation factor (VIF) and related tolerance statistic indicated no concerns with collinearity of the independent variables in both models (VIF values 1.05, 1.35; tolerance values 0.74, 0.96). The assumption of independent errors was deemed tenable from the size of Durbin–Watson statistics (values 1.54, 2.00). We determined that assumptions of normality, linearity and homoscedasticity were met by inspecting residual and scatter plots and histograms generated in SPSS. Shapiro–Wilk and Kolmogorov–Smirnov tests were further performed to test if standardised residuals deviated significantly from normality. For the Bulindi data, assumptions were met after applying a square-root transformation to the dependent variable. We used Mann–Whitney tests to determine if the ranked distribution of crop accessibility scores differed between sites and crop types. We set statistical significance at $p < 0.05$ and all tests were two-tailed.

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Author contributions

M.M. and K.H. contributed equally to all aspects of this work.

Additional information