

1 **Primate crop feeding behaviour, crop protection and conservation**

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6

7 **Abstract**

8 Many species across a range of primate genera, irrespective of dietary and locomotory  
9 specializations, can and will incorporate agricultural crops within their diets. However, while  
10 there is little doubt that rapid, extensive conversion of natural habitats to agricultural areas is  
11 significantly impacting primate populations, primate crop foraging behaviours cannot solely be  
12 understood in terms of animals shifting to cultivated crops to compensate for reduced wild food  
13 availability. To fully understand why, how and when primates might incorporate crops within  
14 their dietary repertoire, we need to examine primate crop foraging behaviour within the context  
15 of their feeding strategies and nutritional ecology. In this paper I briefly outline why terms such  
16 as ‘human-wildlife conflict’ and ‘crop raiding’ are misleading, summarise current knowledge  
17 about primate crop foraging behaviour, and highlight some key areas for future research to  
18 support human-primate coexistence in an increasingly anthropogenic world.

19

## 20 **Introduction**

21

22 Understanding primates' capacity for behavioural and/or dietary flexibility has scientific value  
23 across different contexts from understanding primate responses to anthropogenic change, and  
24 thus their capacity to coexist in the long term with their human neighbours, to developing  
25 effective tools to reduce crop losses from primate foraging and/or trampling activities. Until  
26 recently, research into primate use of anthropogenic foods has focused mostly on the nuisance  
27 value of these behaviours to humans, i.e., crop damage caused by primates feeding on, or  
28 trampling, crops (often referred to as 'crop raiding') (Hill 2017a). Indeed, primates are frequently  
29 identified as topping the lists of wildlife species that damage crops around African and Asian  
30 parks and reserves (Naughton Treves *et al.* 1998). Thus, their capacity to incorporate human  
31 crops into their dietary repertoire becomes a conservation challenge for primatologists.  
32 However, studying the parameters of primate crop foraging behaviour presents an ideal  
33 opportunity to: (i) explore primate capacity for ecological and behavioural flexibility more  
34 generally (Hockings *et al.* 2015), with a view to predicting different species' likely resilience to  
35 coexisting with their human neighbours, and (ii) using this information to develop effective, non-  
36 lethal crop protection strategies, thereby reducing the 'nuisance' feature of primates, and  
37 perhaps facilitating human-primate coexistence in the longer term.

38

39 In this paper I summarise the key information available about primate crop foraging behaviour,  
40 discuss what this information might reveal about primates' capacity to cope with ever increasing  
41 anthropogenic impacts on their habitats, consider how this information can assist in the  
42 development and implementation of crop protection tools and strategies, and outline future  
43 directions for research into human-primate interactions in agricultural landscapes. However,

44 before examining primate crop foraging in detail, I explain why I am using the term ‘crop  
45 foraging’ rather than ‘crop raiding’.

46

#### 47 **A comment on terminology – ‘human-wildlife conflict’ and ‘crop raiding’**

48 A common assumption is that reducing crop losses to primates is key to developing effective  
49 ways of mitigating supposed conflicts between people and their primate neighbours (Hill 2004;  
50 Riley & Priston 2010; Seiler & Robbins 2016). This perspective presumes that these ‘human-  
51 wildlife conflicts’ or ‘human-primate conflicts’ are specifically about the direct costs of sharing  
52 landscapes with wildlife. However, it is now recognised that what are commonly referred to as  
53 ‘human-wildlife conflicts’ are better understood as conflicts between different human stakeholder  
54 groups that arise because of diverse values, agendas, and power relations between these  
55 groups (Madden 2004; Peterson *et al.* 2010). Consequently, using labels such as ‘human-  
56 wildlife conflict’, ‘human-primate conflict’ and ‘crop raiding’ is potentially problematic. These  
57 terms imply “conscious antagonism between wildlife and humans” (Peterson *et al.* 2010, p. 75).  
58 Perhaps more importantly though (at least from a management perspective) their use reinforces  
59 the idea that the animals’ actions are the source or manifestation of the conflict and their human  
60 neighbours the ‘victims’ of these aggressive, forceful or illegal behaviours. This, in turn,  
61 promotes the idea that conflict mitigation is about changing the behaviour of the human and  
62 non-human protagonists rather than addressing the complex, and often deep-rooted, underlying  
63 social conflicts that lie at the core of these issues (Madden and McQuinn 2014; Peterson *et al.*  
64 2010). Likewise, if animal damage is labelled ‘human-wildlife conflict’, it gives people licence to  
65 direct their antagonism towards the animals involved, as ‘perpetrators’ of the ‘conflict’ (Hill  
66 2015), and in some cases this can promote retaliatory killings (Dickman 2010; Jadhav and  
67 Barua 2012; Woodroffe *et al.* 2005). Consequently, where people and wildlife are in competition  
68 over resources the language used to describe these interactions, i.e., ‘human-wildlife conflict’,

69 and the depiction of the animals concerned as 'pests', not only obscures the complex nature of  
70 these 'problems' but may even exacerbate them, further endangering the long-term coexistence  
71 of people and wildlife (Hill 2017b). By contrast, where farmers use these labels to refer to their  
72 experience of crop damage by wildlife, they may either be expressing something about the  
73 experience of losing crops to wildlife (Hill 2015), or using this 'discourse of blame' to express  
74 frustration or dissent over wider societal issues that are not always wildlife-related (Hill 2005; Hill  
75 2015). However, we should be aware that farmers' use of terms like 'crop raid' and 'human-  
76 wildlife conflict' might reflect the labels they hear researchers, wildlife officers, and  
77 conservationists using, and nothing more.

78

### 79 **Primate Crop Foraging**

80 Three Cercopithecoid groups in particular feature in the primate crop foraging literature:  
81 Macaques (*Macaca* spp.), Baboons (*Papio* spp.) (Figure 1) and Vervet monkeys (*Chlorocebus*  
82 spp.). These animals' intelligence and aptitude for social learning, dietary and behavioural  
83 flexibility, manual dexterity, agility and capacity for semi-terrestrial locomotion are all features  
84 thought to make members of these groups particularly adept at incorporating crop foods into  
85 their dietary repertoires (Else 1991; Strum 1994). However, with continuing agricultural  
86 expansion into primate habitats it is increasingly apparent that many species, across a range of  
87 Old World and New World genera, irrespective of their dietary and locomotory specialisations,  
88 can and do include agricultural crops within their diets. Examples include the Yucatan spider  
89 monkey (*Ateles geoffroyi yucatanensis*) (Waters & Ulloa 2007), various capuchin species  
90 (*Sapajus* spp., *Cebus capucinus*) (de Freitas *et al.* 2008; McKinney 2011; Mikich & Liebsch  
91 2014), squirrel monkeys (*Saimiri oerstedii*) (Boinski *et al.* 1998), orangutans (*Pongo* spp.)  
92 (Campbell-Smith *et al.* 2011; Meijaard *et al.* 2011), chimpanzees (*Pan troglodytes*) (Hockings *et*  
93 *al.* 2009; McLennan 20013), mountain gorillas (*Gorilla beringei beringei*) (Madden 2006), ring-

94 tailed lemurs (*Lemur catta*) (LaFleur & Gould 2009), mongoose lemurs (*Eulemur mongoz*)  
95 (Nadhrou *et al.* 2015), Zanzibar red colobus (*Procolobus kirkii*) (Siex & Struhsaker 1999),  
96 purple-faced langurs (*Trachypithecus vetulus*) (Moore *et al.* 2010), and Hanuman langurs  
97 (*Semnopithecus entellus*) (Chhangani *et al.* 2008). It is important to note that this is not an  
98 exhaustive list of species that reportedly forage on crops.

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100 The predominance of semi-terrestrial species in the literature on primate crop foraging is  
101 perhaps partly a consequence of the increased visibility of species that characteristically travel  
102 on the ground; they move in larger, noisier groups, and tend to be larger bodied than more  
103 arboreal species. These characteristics make them more visible to farmers and researchers  
104 alike. For example, farmer detection of primate crop foraging events around the Budongo  
105 Forest Reserve (BFR), Uganda, increased with group size and distance travelled onto farms.  
106 Consequently, farmers consistently underestimated the frequency of crop foraging events,  
107 particularly those carried out by blue monkeys (*Cercopithecus mitis stuhlmanni*) and redtail  
108 monkeys (*Cercopithecus ascanius schmidtii*), and never detected more than 40% of crop  
109 foraging events observed by the research team (Wallace 2010).

110

### 111 Crop Losses

112 Studies of crop damage by wildlife often focus on quantifying losses. Where crop damage has  
113 been systematically monitored across growing seasons the recorded losses vary between farms  
114 and from season to season, even at the same site (Hill 2000: Naughton-Treves *et al.* 1998;  
115 Warren *et al.* 2007). However, systematic monitoring of crop losses is time consuming and  
116 inexact, and it is questionable how useful the results really are because the resulting information  
117 does not accurately reflect what losses mean for farmers, or how people value or use specific

118 crops. Neither does it account for lost opportunity costs associated with crop cultivation or  
119 protection (Hill 2017a). Moreover, estimated amounts of crops lost tell us very little about the  
120 implications of primate crop foraging for people's capacity to tolerate sharing space with these  
121 animals, including their ability or willingness to cope with crop damage. For instance, even  
122 relatively small amounts of damage to particular crops, especially cash crops, can aggravate  
123 farmers considerably, yet farmers may tolerate sizeable losses to other crops (Hill 2005). To  
124 understand people's responses to crop damage we need to consider factors that influence  
125 attitudes towards wildlife, including perceptions of direct economic risks (Chaves & Bicca-  
126 Marques this Issue; McLennan & Hill 2015; Riley & Priston 2010; Spagnoletti *et al.* this Issue),  
127 and perceived physical and psychological threats (Barua *et al.* 2013; McLennan & Hill 2012;  
128 McLennan & Hockings 2016).

129

130 Systematic monitoring of crop damage also tells us little about how, or why, primates  
131 incorporate crops in their diets, though it can provide information about temporal and spatial  
132 patterns of crop use by animals. However, knowing when and where crop damage occurs  
133 within a farm, particularly with respect to natural habitat refuges, paths, houses, crop protection  
134 installations or other features of the landscape, delivers interesting, and potentially useful  
135 information about animal foraging decisions, as well as highlighting where and when crop  
136 protection efforts might be used to best effect (Webber *et al.* 2017). For example, crops within  
137 200m of natural habitat refuges appear most vulnerable to damage from various primate  
138 species (Chhangani *et al.* 2008; Hill 2000; Hiser 2012; Naughton-Treves 1997; Riley 2007; Saj  
139 *et al.* 2001), and particularly where there is a 'hard' boundary between field and natural  
140 vegetation. Very likely this reflects a combination of (i) the degree to which animals perceive  
141 moving into crop lands to be a risky activity, (ii) the level of risk they will accept, and/or (iii) the  
142 value of crops to them. The degree of risk animals are willing to take to access anthropogenic

143 foods is indicative of the relative importance of the resource to these animals. This information  
144 is valuable when designing effective non-lethal methods of crop protection, whereby the aim is  
145 to increase the animals' perceptions of risk associated with crop foraging to the point at which  
146 they are no longer willing to enter fields (Hill & Wallace 2012). Therefore, understanding which  
147 features of a landscape (natural or anthropogenic) contribute to primate perceptions of risk  
148 enables us to manipulate their willingness to engage in 'risky' actions. For example, olive  
149 baboons (*Papio anubis*) around the BFR were reluctant to enter fields where their direct line of  
150 view to the forest edge was obscured. Carefully placed, impenetrable barriers installed at  
151 strategic points on farm boundaries proved effective at deterring baboons from entering these  
152 areas, even when fields were not fully enclosed (Hill & Wallace 2012). Using strategically  
153 placed barriers has a number of benefits over fully enclosing fields at this site, including reduced  
154 financial and labour costs to farmers of installing and maintaining the barriers.

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156 However, it is important to note that should wildlife continue to forage on crops, even in the face  
157 of high levels of risk, this likely indicates they are experiencing significant nutritional shortfalls  
158 when relying solely on wild foods so have little choice but to forage in fields, irrespective of the  
159 risks they might incur. Where this is the case then non-lethal crop protection is unlikely to be  
160 successful, and alternatives including enrichment planting to support animals in the short to  
161 medium term, translocation of 'problem' groups, or even culling to reduce population size should  
162 be considered. Translocation and culling should both be regarded as a 'last resort approach',  
163 i.e., only acceptable if other non-lethal options have failed. Additionally, culling can only be  
164 considered for species that can be legally killed in the country of concern.

165

166 Do all group members feed on crops?



167 Few studies identify the age-sex classes of primates engaging in crop foraging activities.  
168 Observations of olive baboons near Gilgil, Kenya, reveal sub-adult baboons were more likely to  
169 forage on crops than other age groups at this site (Strum 2010). In contrast, around the BFR,  
170 Uganda, adult baboons (Figure 1) primarily engaged in crop foraging and were the age group  
171 most likely to initiate this activity (Wallace & Hill 2012). In southeast Sulawesi, adult and sub-  
172 adult male Buton macaques (*Macaca ochreata brunnescens*) took the lead entering farms to  
173 forage on crops. All age-sex classes entered farms but females and dependent young were  
174 more likely to be observed crop foraging when people and dogs were absent from the farm, i.e.,  
175 during periods when the risks associated with crop foraging were relatively low (Priston *et al.*  
176 2012). Adult male chimpanzees at Bossou, Guinea, spent more time foraging on crops than did  
177 adult females (Hockings *et al.* 2009), and were also more likely to access crops in a village  
178 location than were adult females (Hockings 2007), suggesting adult males were more willing to  
179 engage in potentially risky behaviours than were other age-sex classes at this site (Hockings *et*  
180 *al.* 2012). These differences we observe between sites, as suggested by the results from  
181 Priston *et al.* (2012) and Hockings *et al.* (2012), could reflect differing levels of human presence  
182 or activity at individual sites, and consequently animals' perceived level of risk, rather than  
183 species-specific characteristics. Determining which age-sex groups are willing to enter fields or  
184 plantations, and forage on crops, when combined with observations on vigilance, group spread,  
185 and behaviour states associated with anxiety for instance, could be used as a 'proxy' for (i) the  
186 degree to which animals consider crop foraging at that site to be a risky activity, or (ii) the value  
187 of those crops to the animals concerned.

188

#### 189 Which crops or crop parts are eaten by primates?

190 The range of crop species foraged on by primates is broad, but can vary significantly by species  
191 and site. Primates are recorded foraging on fruits, spices, nuts, leafy and starchy vegetables,

192 grains, peas and beans, sugar cane, and even coffee, tobacco and commercial timber species  
193 (Campbell-Smith *et al.* 2011; Hill 2000; Hockings & McLennan 2012; Hockings & Sousa 2012;  
194 McKinney 2011; Mikich & Liebsch 2014; Siex and Struhsaker 1998; Singh *et al.* 2001). All plant  
195 parts (fruits, leaves, leaf petioles, stems for pith, sap and bark, roots and seeds) can be at risk  
196 (Hill 2017a). For example, baboons in Uganda were observed to consume almost all parts of  
197 maize plants, from extracting newly planted seeds, to feeding on young stems and flower  
198 tassels, and unripe and ripe cobs (Hill 2000). Additionally, not all primates at a particular site  
199 utilise the same species of crops, and/or same plant parts. For example, around BFR, Uganda,  
200 chimpanzees were more likely to target tree fruits and sugar cane than groundnuts or cassava  
201 tubers (Tweheyo *et al.* 2005), whereas baboons ate both groundnuts and cassava tubers at this  
202 site (Hill 2000). This is not unexpected given that chimpanzees are considered specialist  
203 frugivores (Wrangham *et al.* 1998). Similarly, redtail monkeys, olive baboons and chimpanzees  
204 foraging in farms around the edge of Kibale National Park (KNP), Uganda, targeted different  
205 crop types and/crop parts (Naughton-Treves *et al.* 1998). Not surprisingly, primates appear to  
206 make choices about the crop types and parts they access. Yet, important questions remain  
207 about how constrained they are in these choices, what the potential implications for their  
208 capacity to accommodate to changing conditions are, and how might this impact attempts to  
209 reduce crop damage by them.

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211 Detailed knowledge of the range of crops targeted by specific primate species, the degree to  
212 which crop choices reflect species-specific dietary specialisms, and/or primate capacity for  
213 incorporating new crop types into their dietary repertoire, provides an opportunity to explore  
214 species-specific capacity to accommodate to anthropogenic change. For example, a recent  
215 paper confirms that crop selection by chimpanzees at Bossou, Guinea Bissau, which had  
216 experienced long-term exposure to agriculture, was less fruit-focussed compared to crop

217 selection by chimpanzees living in a similarly anthropogenic habitat at Bulindi, Uganda. The  
218 chimpanzees at the Uganda site had been exposed to crops more recently and ignored most  
219 non-fruit crops, unlike chimpanzees at Bossou (McLennan & Hockings 2014). Additionally,  
220 evidence suggests that chimpanzees at Bulindi have incorporated different crop foods into their  
221 dietary repertoire over time (Hiser 2012; McLennan 2013). Furthermore, at Bulindi  
222 chimpanzees were considered far less problematic by farmers, as compared with other wildlife  
223 species, because they did not feed on maize or cassava, both of which are important human  
224 staple crops locally (McLennan & Hill 2012). At other sites in neighbouring districts (Masindi  
225 District and Kabarole District, Uganda) chimpanzees are known to consume maize (Naughton-  
226 Treves *et al.* 1998; Tweheyo *et al.* 2005). Therefore, it is not unreasonable to anticipate that in  
227 the future chimpanzees at Bulindi will include maize in their diet, particularly if wild food  
228 availability declines further. If/when this occurs local tolerance for these animals will, most  
229 likely, be further reduced (Hill, 2005; McLennan & Hill 2012). However, with timely and effective  
230 interventions, to ensure adequate food availability for chimpanzees while simultaneously  
231 encouraging and supporting more effective, humane, non-lethal crop protection methods, this  
232 negative outcome might be averted.

233

234 A common recommendation is that farmers should avoid cultivating those crops that are  
235 particularly vulnerable to crop damage by primates, or at least only grow them at some distance  
236 from primate refuge areas. Notwithstanding the various social, cultural and economic reasons  
237 why many farmers are unlikely to adopt such advice wholesale, there are a number of practical  
238 problems with this suggestion, namely that (i) as in the example above, primates may change  
239 the crop species they target over time, and (ii) at multi-species sites, the range of crops that are  
240 vulnerable to damage by primates may be very great as a consequence of the different feeding  
241 preferences of the various species. However, knowing which crops are likely to be vulnerable to

242 damage by primates could be valuable to farmers, agricultural extension staff, and conservation  
243 and development agencies when considering which crops to promote for local agribusiness  
244 development. There is little point in promoting new crops to improve local incomes as part of a  
245 conservation initiative if the presence of those specific crops acts as an attractant for primates,  
246 encouraging them to visit farms more frequently, further impacting farmer time budgets,  
247 livelihood security and goodwill towards primates, or wildlife more generally.

248

### 249 **Why do primates use crops?**

250 Primates will sometimes go to significant lengths to access anthropogenic foods, including  
251 crops, as demonstrated in a study of vervet monkeys (*Chlorocebus pygerythrus*) in South Africa  
252 (Loudon *et al.* 2014). Stable carbon and nitrogen isotope analysis of hair samples revealed that  
253 a vervet monkey group thought to have only low levels of contact with crops or human foods,  
254 was actually consuming significant levels of these foods, with up to 26% of their diet comprising  
255 C4 plant material (grasses and sedges, including cultivated grains such as corn, millet,  
256 sorghum, and sugar cane). There was no evidence, from direct observation, that the monkeys  
257 ate wild C4 grasses. Further observation revealed they were swimming across a river to forage  
258 on nearby maize crops (Loudon *et al.* 2014). If animals are prepared to go to these lengths to  
259 access crops it suggests these resources are hugely valuable to them.

260

261 A fundamental question is whether primate crop foraging is solely a response to reduced wild  
262 food availability, or does it occur because it confers a nutritional or energetic advantage on  
263 animals that participate? Alternatively, or additionally, do primates find crops more palatable  
264 than wild food alternatives? The answers to these questions will enhance our understanding of  
265 primate foraging decisions and species', or populations', likely resilience in the face of

266 continuing expansion of anthropogenic habitats. Furthermore, and perhaps most importantly,  
267 identifying the factors that drive crop foraging behaviour at different sites provides us with an  
268 opportunity to exploit that information to reduce crop foraging opportunities for these animals  
269 (Hill & Wallace 2012).

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271 An important point to consider is whether wildlife, including primates, forage on farmers crops  
272 because habitat degradation has reduced their access to wild forage to such a degree they  
273 need to utilise crops to survive. Certainly there are instances where wildlife, including primates,  
274 shift to foraging on crops during periods of reduced availability of wild foods. Research from  
275 around KNP, Uganda, confirmed that primates displayed seasonal patterns in their crop  
276 foraging activities. Peak periods of foraging on maize were unconnected to patterns of forest  
277 fruit availability, and the temporal distribution of banana damage was unrelated to rainfall  
278 patterns or fluctuations in maize consumption; instead it was related to periods of low forest fruit  
279 availability (Naughton-Treves *et al.* 1998). Research from Bossou, Guinea, established that  
280 chimpanzees spent more time feeding on crops during periods of wild fruit scarcity (Hockings *et*  
281 *al.* 2009). We see similar seasonal responses to reduced wild food availability from other  
282 species and continents. Tufted capuchins (*Sapajus nigritus*) in southern Brazil were observed  
283 foraging on pine sap much more when wild fruits and seeds were in short supply (Mikich and  
284 Liebsch 2014). Similarly, crop consumption by bearded capuchins (*Sapajus libidinosus*) in  
285 south-eastern Brazil, fluctuated inversely in response to wild fruit availability, with maize and  
286 sugar cane being utilized most heavily by the monkeys during the dry season when wild fruits  
287 were less readily available (de Freitas *et al.* 2008). Nonetheless, even where primates use  
288 crops as a response to seasonal or unpredictable shortfalls in wild food availability, most retain  
289 a significant proportion of wild foods within their diets (Ganzhorn & Abraham 1991; Naughton-  
290 Treves *et al.* 1998; McKinney 2011; McLennan 2013).

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The examples cited above report primates increasing their use of crop foods in response to seasonal reductions in availability of wild foods. At Bulindi, Hoima District, Uganda, there has been very extensive and rapid forest loss, and concomitant decline in natural habitat availability (McLennan & Plumptre 2012). Not surprisingly, as at Bossou, chimpanzees at Bulindi showed increased willingness to engage in crop foraging activities during periods of reduced wild fruit availability (McLennan 2013). However, circumstantial evidence suggests these animals' use of crops at this site has increased significantly in recent times, with farmers reporting damage of field crops by chimpanzees as a comparatively recent phenomenon that broadly corresponds to the period of rapid deforestation locally (Hiser 2012; McLennan & Hill 2012). McLennan intimates that chimpanzees at Bulindi have accommodated rapid anthropogenic impacts on the forest through their inclusion of cultivated crops (McLennan 2013). A further example of primates switching to crop foods in response to reduced wild food availability, this time as a result of natural disaster, comes from the Beza Mahafaly Special Reserve, Madagascar (LaFleur & Gould 2009). Following a cyclone that disrupted the flowering/fruiting cycle of *Tamarindus indicus*, a key food resource for ringtail lemurs (*Lemur catta*), the lemurs included sweet potato leaves in their diet. One group spent 47% of their time foraging on sweet potato leaves; the rest of the time they spent foraging in the forest. The protein and mineral content of potato leaves was lower than that of alternate food resources, and the fibre content higher, yet not only did animals eat them in preference to the alternative, but they also actively defended this novel resource against depredation by a neighbouring group. The authors suggest the reduced processing time and/or taste is most likely why the lemurs preferred sweet potato leaves to wild options but recognise the shift to sweet potato leaves may represent a trade-off between nutritional content and foraging efficiency (LaFleur & Gould 2009).

316 Primate crop foraging cannot always best be explained as a response simply to reduced  
317 availability of natural foods. For example, crop foraging activities of orangutans (*Pongo abeli*) in  
318 Sumatra were linked specifically to the availability of cultivated fruits and not to reduced  
319 availability of wild fruits (Campbell-Smith *et al.* 2010). Similarly, mountain gorillas use of crops  
320 (banana pith and eucalyptus bark) appeared to be more a matter of preference rather than need  
321 at Bwindi Impenetrable Forest National Park, Uganda. Analysis of gorilla ranging behaviour  
322 revealed that animals were drawn to foods outside the park in response to their availability  
323 (crops and wild herbaceous plants in plantations and uncultivated land) and not as a response  
324 to reduced wild food availability within the national park (Seiler and Robbins 2016).

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326 One way to explore these questions further is through the lens of optimal foraging theory. If  
327 primate crop foraging behaviour is a strategy for optimising animals' foraging returns then it  
328 should reflect a balance between the potential costs and benefits of incorporating crops within  
329 animal diets, where overall benefits are reflected in animals' nutritional status and/or  
330 reproductive success. Crops tend to be spatially and temporally highly clumped (Strum 1994),  
331 relatively easy to process, and contain less nondigestible fibre than do wild foods (Rode *et al.*  
332 2006). They also tend to be highly predictable during any planting season, and may require  
333 less handling time than certain wild foods. These are all factors that enhance foraging efficiency  
334 (Strum 1994). Potential costs associated with crop foraging include primates being at increased  
335 risk of injury or death, as a consequence of farmers trying to protect their crops, and/or  
336 increased exposure to pathogens as a result of spending time in close proximity with people and  
337 their livestock.

338  
339 To date there are very few studies that examine primate crop foraging behaviour within an  
340 analytical framework that considers the balance between likely costs and benefits of the animals

341 actions. A long-term study of baboon groups at Gilgil, Kenya, compared life history variables in  
342 animals with access to anthropogenic foods (crops and garbage) to those of animals who only  
343 had access to wild foods (Strum 2010). Baboons with access to anthropogenic foods spent less  
344 time feeding and more time resting, and had a smaller home range area than the group with  
345 access to wild foods only. Moreover, inter-birth intervals were shorter in females utilising human  
346 foods compared with those eating only wild foods. There was no evidence overall of increased  
347 mortality among the group foraging on anthropogenic foods as a consequence of increased risk  
348 of injury, death or disease, though mortality rates in this group were initially raised but declined  
349 over time, suggesting animals adjusted to any risks associated with crop and garbage foraging  
350 (Strum 2010). The highest strongyle (gastrointestinal nematode parasites) egg counts were  
351 recorded from those animals without access to anthropogenic foods (Eley *et al.* 1989). Overall,  
352 the advantages associated with foraging on human foods at this site, appeared to outweigh any  
353 costs the animals incurred by adopting this behaviour (Strum 2010).

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355 The olive baboons of Gashaka Gumti National Park, Nigeria, have been the focus of a number  
356 of studies comparing groups with access to crop foods to those without. At Gashaka Gumpti  
357 crop foraging appears to provide a buffer against seasonal nutritional stress (MacLarnon *et al.*  
358 2015). Additionally, those baboons who forage on crops also have higher energy intake and  
359 energy balance (Lodge *et al.* 2013) and higher fertility and lower mortality rates (Higham *et al.*  
360 2009; Lodge *et al.* 2013), which may reflect higher nutritional status. There were also  
361 differences in gastrointestinal parasite loads and species diversity between the two groups.  
362 Animals that foraged on crops had reduced helminthic parasite loads compared with those  
363 recorded for animals that fed exclusively on wild foods (Weyher *et al.* 2006). This result may  
364 reflect the higher nutritional status of the crop foraging group that enables them to combat  
365 parasite infection more effectively (Eley *et al.* 1989; Weyher *et al.* 2006). Crop foraging at Gilgil



366 and Gashaka Gumpti NP appears to confer an energetic or nutritional advantage on baboons  
367 over and above the impacts of costs they might incur when foraging on crops. We should,  
368 therefore, take these factors into consideration when examining primate capacity for  
369 accommodation to anthropogenic change and willingness/capacity to engage in potentially risky  
370 behaviours. We can also use this information to think more carefully about how to manipulate  
371 primate behaviour prior to and during crop foraging events; here we need to ensure that the  
372 perceived risks of crop foraging outweigh any likely short-term and long-term benefits animals  
373 might gain.

374

375 To make full use of this information requires some further detail. For example, understanding  
376 how crop foods contribute to primate nutritional ecology and primate efforts to meet their macro-  
377 and micronutrient requirements, would enable farmers to fine-tune their own cropping strategies  
378 to minimise crop losses. To date there are relatively few studies of crop foraging behaviour in  
379 primates to date that have analysed primate crop feeding strategies from a nutritional ecology  
380 perspective. The few that have been published tend to approach the question from an energy  
381 maximisation perspective, but more considered analysis exploring the role of crop foods in  
382 protein maximisation, avoidance of plant secondary metabolites, regulation of fibre intake, or  
383 nutrient balancing (Felton *et al.* 2009) could generate a clearer understanding of how or why  
384 primates utilise crops.

385

386 A study of Chacma baboons (*Papio ursinus*), in the Cape Peninsula, South Africa,  
387 demonstrated that baboons experience seasonal fluctuations in their time budgets and dietary  
388 intake (Van Doorn *et al.* 2010). The baboons responded to reduced food availability and/or  
389 reduced food quality during the winter months by increasing their intake of energy dense, ostrich

390 pellets (commercial food used on ostrich farms). Although winter is a time of relative wild food  
391 scarcity at this site the availability of an abundant fallback food within ostrich pens meant the  
392 baboons actually reduced their time spent feeding during the winter as compared with summer  
393 when fynbos, flowers, fruits and seeds were abundant. Wild foods required more handling time  
394 than ostrich pellets, therefore by incorporating ostrich pellets within their diet baboons were  
395 taking the opportunity to optimise their foraging efficiency, rather than necessarily simply  
396 responding to seasonal food shortage (Van Doorn *et al.* (2010). Studies of food enhanced  
397 primate groups report changes to activity budgets, including reduced time spent feeding and  
398 increased time spent resting (Forthman-Quick & Demment 1988; Saj *et al.* 1999), as might be  
399 expected where animals have ready access to spatially and temporally clumped, energy dense  
400 food sources. However, chimpanzees and orangutans had longer day range lengths on days  
401 they foraged in crops (Hockings *et al.* 2012; Campbell-Smith *et al.* 2011), and chimpanzees also  
402 invested more time in feeding activities on crop foraging days (Hockings *et al.* 2012). By  
403 contrast white-faced capuchins (*Cebus capucinus*) with access to anthropogenic foods occupied  
404 a larger home range area than a group without access to human foods, but both groups had  
405 similar activity budgets (McKinney 2011). Furthermore, a study of food-enhanced long-tailed  
406 macaques (*Macaca fascicularis*) in Singapore revealed that the group with the highest  
407 proportion of human foods in their diet devoted less of their time to feeding on wild foods, less  
408 time resting and more time travelling than the group with reduced access to anthropogenic  
409 foods (Sha & Hanya 2013). Increased day travel length, i.e., increased time spent travelling, in  
410 groups that access anthropogenic foods (crops, garbage dumps, intentional provisioning sites)  
411 might reflect the enhanced caloric value of these food sources to animals.

412

413 A further alternative is that primates might be trying to achieve a balance between energetic  
414 returns and other nutritional constraints, via their use of crop foods. Riley and colleagues, in

415 their research on Tonkean macaques (*Macaca tonkeana*) in Sulawesi, Indonesia, compared  
416 nutritional quality of forest fruits with cacao pulp, a food frequently eaten by the macaques.  
417 Forest fruits had higher protein, lipid and nondigestible fibre levels, but lower digestible  
418 carbohydrate content than cacao, and the average energy content of forest fruits was  
419 considerably lower than that of cacao pulp. The authors suggest that by selecting cacao in  
420 preference to wild fruits the macaques were opting to maximise their energy intake and  
421 minimise their intake of nondigestible fibre rather than maximise protein or lipid intake (Riley *et*  
422 *al.* 2013). Similarly, crop foods eaten by chimpanzees at Bulindi, Uganda, have higher sugar  
423 content and lower fibre and secondary compounds compared to equivalent wild food items  
424 (McLennan & Ganzhorn, this issue).

425

426 Alternatively, primates might incorporate crops within their diets to balance micronutrients,  
427 rather than maximise energy balance. Nutritional analysis of wild and crop foods eaten by  
428 elephants in KNP, Uganda, showed that crop foods had higher sodium, and reduced levels of  
429 fibre and secondary compounds as compared with wild foods eaten by elephants (Rode *et al.*  
430 2006). The authors concluded that, because wild forage has a low mineral content, elephant  
431 crop foraging decisions were influenced, at least in part, by a drive to access sodium-rich foods  
432 (Rode *et al.* 2006). However, a similar analysis of primate diets at KNP revealed that mineral  
433 levels in wild primate foods were generally higher than those in local crops, with the exception of  
434 sodium and iron content (Rode *et al.* 2003). A combination of factors very likely drive crop  
435 foraging patterns but additional research into the impacts of mineral nutrition on animal foraging  
436 strategies may prove useful for developing innovative ways of enticing animals away from crops  
437 using sodium blocks for instance or enhancing the effectiveness of buffer zones through careful  
438 planting of crops that are high in fibre and secondary compounds, and low in sodium for  
439 example (Rode *et al.* 2003, 2006).

440

441 **Future directions**

442 Understanding primate feeding strategies and food choices in increasingly human-dominated  
443 habitats is crucial for examining primate resilience to anthropogenic change. Future research  
444 should focus on the following:

- 445 • Collating comprehensive information on the full range of crop species included in key  
446 primate diets. This information would be valuable to inform agricultural extension  
447 officers, wildlife managers, farmers and conservation organisations, and especially  
448 where attempts are made to introduce novel crops to a site with a view to enhancing  
449 farming livelihoods as part of a conservation programme. To my knowledge this  
450 information has, to date, only been assembled for chimpanzees (see Hockings &  
451 McLennan 2012). Other primate groups that would merit similar careful analysis are  
452 baboons, macaques and capuchins.
- 453 • Developing predictive models of primate behavioural responses to risk associated with  
454 crop foraging behaviour. Such models could help identify ways to modify landscapes to  
455 make them appear more 'risky' for primates, as a way of encouraging animals to forage  
456 elsewhere. Additionally, it should be possible to identify crop damage 'hot spots' that  
457 should be a priority for crop protection efforts, and/or ideal locations for enrichment  
458 planting and natural habitat protection to ensure adequate food resource availability of  
459 high value wild foods to 'draw' primates away from cultivated areas.
- 460 • Exploring primate crop foraging activity within a nutritional ecology framework to  
461 understand more comprehensively when and why primates incorporate crops within their  
462 diets. This information would enhance our understanding of primate capacity to cope  
463 with changing resource availability, and provide additional, nuanced detail, to inform  
464 initiatives to support primates under nutritional stress. Furthermore, it could be used to

465 develop enhanced foraging opportunities to encourage primates to choose alternatives  
466 to foraging on crops.

- 467 • Adopting a comparative approach to explore lessons learned from studies of crop  
468 foraging in other wildlife species, and whether they can further our understanding of  
469 primate behaviour, especially in the context of animals' perception of risk and their  
470 feeding ecology.

471

## 472 **Conclusions**

473 There is no doubt that rapid and extensive conversion of natural habitats to agricultural areas is  
474 having significant impacts on primate populations throughout their range, but some species  
475 appear able to accommodate to such changes, at least to a degree. However, while it is  
476 tempting to assume that primate crop foraging activity is a coping mechanism in increasingly  
477 anthropogenic landscapes, these behaviours cannot solely be understood in terms of animals  
478 shifting to cultivated crops to compensate for reduced wild food availability. Indeed, evidence is  
479 accruing to support the idea that incorporating anthropogenic foods within their diets is a way of  
480 optimising nutritional sufficiency, at least in some instances.

481

482 Richard and colleagues have proposed that the introduction of agricultural and livestock  
483 husbandry over the last 10,000 years created new habitats, providing 'weed' species of  
484 macaques with novel feeding opportunities, perhaps at the expense of climax forest specialists  
485 (Richard *et al.* 1989), where 'weed' species are those that coexist very successfully with  
486 humans. It is not unreasonable therefore to speculate that something similar happened with  
487 certain African cercopithecine species who, like macaques, exploit anthropogenic habitats very  
488 effectively. Primate capacity to accommodate to, and even exploit, anthropogenic change

489 impacts their current and likely future distribution. Investigating primate behavioural and  
490 ecological capacity for flexibility in crop foraging contexts provides an opportunity to examine, in  
491 real time, how primates respond to changing ecological opportunities, develop models to identify  
492 tipping points beyond which primate populations are unable to cope, and developing effective,  
493 non-lethal crop protection strategies. Given the need to accommodate people and wildlife within  
494 increasingly crowded landscapes, such challenges are all important when considering the long  
495 term sustainability of people-primate coexistence, and realistic and effective strategies to  
496 support future coexistence.

497

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