Primate crop feeding behaviour, crop protection and conservation

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Abstract

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

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

In this paper I summarise the key information available about primate crop foraging behaviour, discuss what this information might reveal about primates’ capacity to cope with ever increasing anthropogenic impacts on their habitats, consider how this information can assist in the development and implementation of crop protection tools and strategies, and outline future directions for research into human-primate interactions in agricultural landscapes. However,
before examining primate crop foraging in detail, I explain why I am using the term ‘crop foraging’ rather than ‘crop raiding’.

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

A common assumption is that reducing crop losses to primates is key to developing effective ways of mitigating supposed conflicts between people and their primate neighbours (Hill 2004; Riley & Priston 2010; Seiler & Robbins 2016). This perspective presumes that these ‘human-wildlife conflicts’ or ‘human-primate conflicts’ are specifically about the direct costs of sharing landscapes with wildlife. However, it is now recognised that what are commonly referred to as ‘human-wildlife conflicts’ are better understood as conflicts between different human stakeholder groups that arise because of diverse values, agendas, and power relations between these groups (Madden 2004; Peterson et al. 2010). Consequently, using labels such as ‘human-wildlife conflict’, ‘human-primate conflict’ and ‘crop raiding’ is potentially problematic. These terms imply “conscious antagonism between wildlife and humans” (Peterson et al. 2010, p. 75).

Perhaps more importantly though (at least from a management perspective) their use reinforces the idea that the animals’ actions are the source or manifestation of the conflict and their human neighbours the ‘victims’ of these aggressive, forceful or illegal behaviours. This, in turn, promotes the idea that conflict mitigation is about changing the behaviour of the human and non-human protagonists rather than addressing the complex, and often deep-rooted, underlying social conflicts that lie at the core of these issues (Madden and McQuinn 2014; Peterson et al. 2010). Likewise, if animal damage is labelled ‘human-wildlife conflict’, it gives people licence to direct their antagonism towards the animals involved, as ‘perpetrators’ of the ‘conflict’ (Hill 2015), and in some cases this can promote retaliatory killings (Dickman 2010; Jadhav and Barua 2012; Woodroffe et al. 2005). Consequently, where people and wildlife are in competition over resources the language used to describe these interactions, i.e., ‘human-wildlife conflict’,
and the depiction of the animals concerned as ‘pests’, not only obscures the complex nature of these ‘problems’ but may even exacerbate them, further endangering the long-term coexistence of people and wildlife (Hill 2017b). By contrast, where farmers use these labels to refer to their experience of crop damage by wildlife, they may either be expressing something about the experience of losing crops to wildlife (Hill 2015), or using this ‘discourse of blame’ to express frustration or dissent over wider societal issues that are not always wildlife-related (Hill 2005; Hill 2015). However, we should be aware that farmers’ use of terms like ‘crop raid’ and ‘human-wildlife conflict’ might reflect the labels they hear researchers, wildlife officers, and conservationists using, and nothing more.

Primate Crop Foraging

Three Cercopithecoid groups in particular feature in the primate crop foraging literature: Macaques (*Macaca* spp.), Baboons (*Papio* spp.) (Figure 1) and Vervet monkeys (*Chlorocebus* spp.). These animals’ intelligence and aptitude for social learning, dietary and behavioural flexibility, manual dexterity, agility and capacity for semi-terrestrial locomotion are all features thought to make members of these groups particularly adept at incorporating crop foods into their dietary repertoires (Else 1991; Strum 1994). However, with continuing agricultural expansion into primate habitats it is increasingly apparent that many species, across a range of Old World and New World genera, irrespective of their dietary and locomotory specialisations, can and do include agricultural crops within their diets. Examples include the Yucatan spider monkey (*Ateles geoffroyi yucatanensis*) (Waters & Ulloa 2007), various capuchin species (*Sapajus* spp., *Cebus capucinus*) (de Freitas et al. 2008; McKinney 2011; Mikich & Liebsch 2014), squirrel monkeys (*Saimiri oerstedii*) (Boinski et al. 1998), orangutans (*Pongo* spp.) (Campbell-Smith et al. 2011; Meijaard et al. 2011), chimpanzees (*Pan troglodytes*) (Hockings et al. 2009; McLennan 20013), mountain gorillas (*Gorilla beringei beringei*) (Madden 2006), ring-
tailed lemurs (*Lemur catta*) (LaFleur & Gould 2009), mongoose lemurs (*Eulemur mongoz*) (Nadhurou et al. 2015), Zanzibar red colobus (*Procolobus kirkii*) (Siex & Struhsaker 1999), purple-faced langurs (*Trachypithecus vetulus*) (Moore et al. 2010), and Hanuman langurs (*Semnopithecus entellus*) (Chhangani et al. 2008). It is important to note that this is not an exhaustive list of species that reportedly forage on crops.

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

**Crop Losses**

Studies of crop damage by wildlife often focus on quantifying losses. Where crop damage has been systematically monitored across growing seasons the recorded losses vary between farms and from season to season, even at the same site (Hill 2000; Naughton-Treves et al. 1998; Warren et al. 2007). However, systematic monitoring of crop losses is time consuming and inexact, and it is questionable how useful the results really are because the resulting information does not accurately reflect what losses mean for farmers, or how people value or use specific
crops. Neither does it account for lost opportunity costs associated with crop cultivation or protection (Hill 2017a). Moreover, estimated amounts of crops lost tell us very little about the implications of primate crop foraging for people’s capacity to tolerate sharing space with these animals, including their ability or willingness to cope with crop damage. For instance, even relatively small amounts of damage to particular crops, especially cash crops, can aggravate farmers considerably, yet farmers may tolerate sizeable losses to other crops (Hill 2005). To understand people’s responses to crop damage we need to consider factors that influence attitudes towards wildlife, including perceptions of direct economic risks (Chaves & Bicca-Marques this Issue; McLennan & Hill 2015; Riley & Priston 2010; Spagnoletti et al. this Issue), and perceived physical and psychological threats (Barua et al. 2013; McLennan & Hill 2012; McLennan & Hockings 2016).

Systematic monitoring of crop damage also tells us little about how, or why, primates incorporate crops in their diets, though it can provide information about temporal and spatial patterns of crop use by animals. However, knowing when and where crop damage occurs within a farm, particularly with respect to natural habitat refuges, paths, houses, crop protection installations or other features of the landscape, delivers interesting, and potentially useful information about animal foraging decisions, as well as highlighting where and when crop protection efforts might be used to best effect (Webber et al. 2017). For example, crops within 200m of natural habitat refuges appear most vulnerable to damage from various primate species (Chhangani et al. 2008; Hill 2000; Hiser 2012; Naughton-Treves 1997; Riley 2007; Saj et al. 2001), and particularly where there is a ‘hard’ boundary between field and natural vegetation. Very likely this reflects a combination of (i) the degree to which animals perceive moving into crop lands to be a risky activity, (ii) the level of risk they will accept, and/or (iii) the value of crops to them. The degree of risk animals are willing to take to access anthropogenic
foods is indicative of the relative importance of the resource to these animals. This information is valuable when designing effective non-lethal methods of crop protection, whereby the aim is to increase the animals’ perceptions of risk associated with crop foraging to the point at which they are no longer willing to enter fields (Hill & Wallace 2012). Therefore, understanding which features of a landscape (natural or anthropogenic) contribute to primate perceptions of risk enables us to manipulate their willingness to engage in ‘risky’ actions. For example, olive baboons (*Papio anubis*) around the BFR were reluctant to enter fields where their direct line of view to the forest edge was obscured. Carefully placed, impenetrable barriers installed at strategic points on farm boundaries proved effective at deterring baboons from entering these areas, even when fields were not fully enclosed (Hill & Wallace 2012). Using strategically placed barriers has a number of benefits over fully enclosing fields at this site, including reduced financial and labour costs to farmers of installing and maintaining the barriers.

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

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

Which crops or crop parts are eaten by primates?

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

Detailed knowledge of the range of crops targeted by specific primate species, the degree to
which crop choices reflect species-specific dietary specialisms, and/or primate capacity for
incorporating new crop types into their dietary repertoire, provides an opportunity to explore
species-specific capacity to accommodate to anthropogenic change. For example, a recent
paper confirms that crop selection by chimpanzees at Bossou, Guinea Bissau, which had
experienced long-term exposure to agriculture, was less fruit-focussed compared to crop
selection by chimpanzees living in a similarly anthropogenic habitat at Bulindi, Uganda. The chimpanzees at the Uganda site had been exposed to crops more recently and ignored most non-fruit crops, unlike chimpanzees at Bossou (McLennan & Hockings 2014). Additionally, evidence suggests that chimpanzees at Bulindi have incorporated different crop foods into their dietary repertoire over time (Hiser 2012; McLennan 2013). Furthermore, at Bulindi chimpanzees were considered far less problematic by farmers, as compared with other wildlife species, because they did not feed on maize or cassava, both of which are important human staple crops locally (McLennan & Hill 2012). At other sites in neighbouring districts (Masindi District and Kabarole District, Uganda) chimpanzees are known to consume maize (Naughton-Treves et al. 1998; Tweheyo et al. 2005). Therefore, it is not unreasonable to anticipate that in the future chimpanzees at Bulindi will include maize in their diet, particularly if wild food availability declines further. If/when this occurs local tolerance for these animals will, most likely, be further reduced (Hill, 2005; McLennan & Hill 2012). However, with timely and effective interventions, to ensure adequate food availability for chimpanzees while simultaneously encouraging and supporting more effective, humane, non-lethal crop protection methods, this negative outcome might be averted.

A common recommendation is that farmers should avoid cultivating those crops that are particularly vulnerable to crop damage by primates, or at least only grow them at some distance from primate refuge areas. Notwithstanding the various social, cultural and economic reasons why many farmers are unlikely to adopt such advice wholesale, there are a number of practical problems with this suggestion, namely that (i) as in the example above, primates may change the crop species they target over time, and (ii) at multi-species sites, the range of crops that are vulnerable to damage by primates may be very great as a consequence of the different feeding preferences of the various species. However, knowing which crops are likely to be vulnerable to
damage by primates could be valuable to farmers, agricultural extension staff, and conservation
and development agencies when considering which crops to promote for local agribusiness
development. There is little point in promoting new crops to improve local incomes as part of a
conservation initiative if the presence of those specific crops acts as an attractant for primates,
encouraging them to visit farms more frequently, further impacting farmer time budgets,
livelihood security and goodwill towards primates, or wildlife more generally.

**Why do primates use crops?**

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

A fundamental question is whether primate crop foraging is solely a response to reduced wild
food availability, or does it occur because it confers a nutritional or energetic advantage on
animals that participate? Alternatively, or additionally, do primates find crops more palatable
than wild food alternatives? The answers to these questions will enhance our understanding of
primate foraging decisions and species’, or populations’, likely resilience in the face of
continuing expansion of anthropogenic habitats. Furthermore, and perhaps most importantly, identifying the factors that drive crop foraging behaviour at different sites provides us with an opportunity to exploit that information to reduce crop foraging opportunities for these animals (Hill & Wallace 2012).

An important point to consider is whether wildlife, including primates, forage on farmers crops because habitat degradation has reduced their access to wild forage to such a degree they need to utilise crops to survive. Certainly there are instances where wildlife, including primates, shift to foraging on crops during periods of reduced availability of wild foods. Research from around KNP, Uganda, confirmed that primates displayed seasonal patterns in their crop foraging activities. Peak periods of foraging on maize were unconnected to patterns of forest fruit availability, and the temporal distribution of banana damage was unrelated to rainfall patterns or fluctuations in maize consumption; instead it was related to periods of low forest fruit availability (Naughton-Treves et al. 1998). Research from Bossou, Guinea, established that chimpanzees spent more time feeding on crops during periods of wild fruit scarcity (Hockings et al. 2009). We see similar seasonal responses to reduced wild food availability from other species and continents. Tufted capuchins (Sapajus nigritus) in southern Brazil were observed foraging on pine sap much more when wild fruits and seeds were in short supply (Mikich and Liebsch 2014). Similarly, crop consumption by bearded capuchins (Sapajus libidinosus) in south-eastern Brazil, fluctuated inversely in response to wild fruit availability, with maize and sugar cane being utilized most heavily by the monkeys during the dry season when wild fruits were less readily available (de Freitas et al. 2008). Nonetheless, even where primates use crops as a response to seasonal or unpredictable shortfalls in wild food availability, most retain a significant proportion of wild foods within their diets (Ganzhorn & Abraham 1991; Naughton-Treves et al. 1998; McKinney 2011; McLennan 2013).
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).
Primate crop foraging cannot always best be explained as a response simply to reduced availability of natural foods. For example, crop foraging activities of orangutans (*Pongo abelii*) in Sumatra were linked specifically to the availability of cultivated fruits and not to reduced availability of wild fruits (Campbell-Smith *et al.* 2010). Similarly, mountain gorillas use of crops (banana pith and eucalyptus bark) appeared to be more a matter of preference rather than need at Bwindi Impenetrable Forest National Park, Uganda. Analysis of gorilla ranging behaviour revealed that animals were drawn to foods outside the park in response to their availability (crops and wild herbaceous plants in plantations and uncultivated land) and not as a response to reduced wild food availability within the national park (Seiler and Robbins 2016).

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

To date there are very few studies that examine primate crop foraging behaviour within an analytical framework that considers the balance between likely costs and benefits of the animals.
actions. A long-term study of baboon groups at Gilgil, Kenya, compared life history variables in animals with access to anthropogenic foods (crops and garbage) to those of animals who only had access to wild foods (Strum 2010). Baboons with access to anthropogenic foods spent less time feeding and more time resting, and had a smaller home range area than the group with access to wild foods only. Moreover, inter-birth intervals were shorter in females utilising human foods compared with those eating only wild foods. There was no evidence overall of increased mortality among the group foraging on anthropogenic foods as a consequence of increased risk of injury, death or disease, though mortality rates in this group were initially raised but declined over time, suggesting animals adjusted to any risks associated with crop and garbage foraging (Strum 2010). The highest strongyle (gastrointestinal nematode parasites) egg counts were recorded from those animals without access to anthropogenic foods (Eley et al. 1989). Overall, the advantages associated with foraging on human foods at this site, appeared to outweigh any costs the animals incurred by adopting this behaviour (Strum 2010).

The olive baboons of Gashaka Gumti National Park, Nigeria, have been the focus of a number of studies comparing groups with access to crop foods to those without. At Gashaka Gumti crop foraging appears to provide a buffer against seasonal nutritional stress (MacLarnon et al. 2015). Additionally, those baboons who forage on crops also have higher energy intake and energy balance (Lodge et al. 2013) and higher fertility and lower mortality rates (Higham et al. 2009; Lodge et al. 2013), which may reflect higher nutritional status. There were also differences in gastrointestinal parasite loads and species diversity between the two groups. Animals that foraged on crops had reduced helminthic parasite loads compared with those recorded for animals that fed exclusively on wild foods (Weyher et al. 2006). This result may reflect the higher nutritional status of the crop foraging group that enables them to combat parasite infection more effectively (Eley et al. 1989; Weyher et al. 2006). Crop foraging at Gilgil
and Gashaka Gumti NP appears to confer an energetic or nutritional advantage on baboons over and above the impacts of costs they might incur when foraging on crops. We should, therefore, take these factors into consideration when examining primate capacity for accommodation to anthropogenic change and willingness/capacity to engage in potentially risky behaviours. We can also use this information to think more carefully about how to manipulate primate behaviour prior to and during crop foraging events; here we need to ensure that the perceived risks of crop foraging outweigh any likely short-term and long-term benefits animals might gain.

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

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

A further alternative is that primates might be trying to achieve a balance between energetic returns and other nutritional constraints, via their use of crop foods. Riley and colleagues, in
their research on Tonkean macaques (*Macaca tonkeana*) in Sulawesi, Indonesia, compared nutritional quality of forest fruits with cacao pulp, a food frequently eaten by the macaques. Forest fruits had higher protein, lipid and nondigestible fibre levels, but lower digestible carbohydrate content than cacao, and the average energy content of forest fruits was considerably lower than that of cacao pulp. The authors suggest that by selecting cacao in preference to wild fruits the macaques were opting to maximise their energy intake and minimise their intake of nondigestible fibre rather than maximise protein or lipid intake (Riley *et al.* 2013). Similarly, crop foods eaten by chimpanzees at Bulindi, Uganda, have higher sugar content and lower fibre and secondary compounds compared to equivalent wild food items (McLennan & Ganzhorn, this issue).

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

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

- Collating comprehensive information on the full range of crop species included in key primate diets. This information would be valuable to inform agricultural extension officers, wildlife managers, farmers and conservation organisations, and especially where attempts are made to introduce novel crops to a site with a view to enhancing farming livelihoods as part of a conservation programme. To my knowledge this information has, to date, only been assembled for chimpanzees (see Hockings & McLennan 2012). Other primate groups that would merit similar careful analysis are baboons, macaques and capuchins.

- Developing predictive models of primate behavioural responses to risk associated with crop foraging behaviour. Such models could help identify ways to modify landscapes to make them appear more 'risky' for primates, as a way of encouraging animals to forage elsewhere. Additionally, it should be possible to identify crop damage 'hot spots' that should be a priority for crop protection efforts, and/or ideal locations for enrichment planting and natural habitat protection to ensure adequate food resource availability of high value wild foods to ‘draw’ primates away from cultivated areas.

- Exploring primate crop foraging activity within a nutritional ecology framework to understand more comprehensively when and why primates incorporate crops within their diets. This information would enhance our understanding of primate capacity to cope with changing resource availability, and provide additional, nuanced detail, to inform initiatives to support primates under nutritional stress. Furthermore, it could be used to
develop enhanced foraging opportunities to encourage primates to choose alternatives
to foraging on crops.

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

Conclusions

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

Richard and colleagues have proposed that the introduction of agricultural and livestock
husbandry over the last 10,000 years created new habitats, providing ‘weed’ species of
macaques with novel feeding opportunities, perhaps at the expense of climax forest specialists
(Richard et al. 1989), where ‘weed’ species are those that coexist very successfully with
humans. It is not unreasonable therefore to speculate that something similar happened with
certain African cercopithecine species who, like macaques, exploit anthropogenic habitats very
effectively. Primate capacity to accommodate to, and even exploit, anthropogenic change
impacts their current and likely future distribution. Investigating primate behavioural and ecological capacity for flexibility in crop foraging contexts provides an opportunity to examine, in real time, how primates respond to changing ecological opportunities, develop models to identify tipping points beyond which primate populations are unable to cope, and developing effective, non-lethal crop protection strategies. Given the need to accommodate people and wildlife within increasingly crowded landscapes, such challenges are all important when considering the long term sustainability of people-primate coexistence, and realistic and effective strategies to support future coexistence.

References


