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Baboon and vervet monkey crop-foraging behaviors on a commercial South African farm: preliminary implications for damage mitigation

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Abstract: Conflict between crop farmers and wild nonhuman primates is a worldwide conservation issue of increasing concern. Most of the research on wild primate crop foraging has so far focused on the conflicts with subsistence agriculture. Crop damage caused by primate foraging in large-scale commercial agriculture is also a major facet of human–wildlife conflict. Despite its increasing severity, there are very few published accounts of on-farm wild primate crop-foraging behavior or effective techniques to deter primates from field crops on commercial farms. To address this knowledge gap and identify some mitigation strategies, we used direct observation from a hide to collect behaviors and interspecific interactions between chacma baboons (*Papio ursinus*; baboons) and vervet monkeys (*Chlorocebus pygerythrus*; vervets) foraging in a 1-ha butternut squash (*Cucurbita moschata*) field for 4 months (May to August) in 2013 on a 564-ha commercial farm in the Blouberg District of South Africa. Baboons caused the most crop damage, foraged on crops more in the mornings, and their rates of crop foraging were influenced primarily by natural vegetation productivity. Vervet monkey rates of crop foraging were primarily influenced by the presence of baboons. When baboons or vervets visited the farm, half of the visits did not involve crop foraging, and vervets were more likely to crop forage when they visited than baboons. Based on this preliminary study, we make recommendations for crop farmers to improve the effectiveness of current deterrent methods. These include increasing deterrent efforts when natural vegetation drops below a normalized difference vegetation index value of 0.32, especially during the hours before midday, chasing baboons and vervets farther from the farm rather than just out of crop fields, and increasing the perceived mortality risk of field guards. These recommendations should be evaluated to determine effectiveness before being adopted on a wider scale.

Keywords: baboon, *Chlorocebus pygerythrus*, crop damage, crop raiding, foraging behavior, human–wildlife conflicts, mitigation, *Papio ursinus*, South Africa, vervet monkey, wildlife damage management

INCREASING HUMAN–WILDLIFE conflicts is now recognized worldwide as an issue of conservation concern (Anand and Radhakrishna 2017). One of the most common and widespread conflicts between humans and wildlife takes the form of crop foraging or crop raiding (Hill 1998, Strum 2010, Ling 2016, Fehlmann et al. 2017*a*). Crop foraging (often termed crop raiding) can be defined as free-ranging animals moving from their natural habitat into agricultural land to feed on the produce or crops that humans grow for their own consumption (Hill 2017*a*). Crop foraging is not a new phenomenon and is as old as agriculture itself (Naughton-Treves 1997,

Hill 2005, Lamarque et al. 2008). Crop foraging by free-ranging animals not only causes economic losses, but may result in increased wildlife mortalities through lethal human retaliation (Mackenzie et al. 2015, Ango et al. 2016, Anand et al. 2018). Thus, crop foraging is a high-risk behavior for many wildlife species.

Wild nonhuman primates (hereafter primates) that forage on the crops of subsistence farmers are particularly problematic because they threaten farmers' livelihoods (Hill 2002, Tweheyo et al. 2005, Campbell-Smith et al. 2010). Baboons (*Papio* spp.) are often cited as the most damaging of all primate crop foraging species for subsistence agriculture (Naughton-Treves 1997, Tweheyo et al. 2005, McLennan and Hill 2012, Hill 2018). Farmers often have little success preventing crop damage by primates (Mason 1998, Mackenzie and Ahabyona 2012, MacLarnon et al. 2015, Fehlmann et al. 2017*b*). As a result, subsistence farmers often feel they are left with no other option than lethal control (Starin 1989, Webber 2006, Hill and Webber 2010, Mackenzie et al. 2015).

Most of the research on primate crop foraging has so far focused on the conflict between primates and subsistence farmers (Tchamba 1996, Siex and Struhsaker 1999, Nahallage et al. 2008, Waters 2015). Primate damage to commercial agriculture presents conservation challenges of its own. Here we define commercial farming as the production of crops and farm animals for sale, usually with the use of modern technology, and therefore include family farms that send produce to national and international markets as well as large corporate farms. While commercial farmer livelihoods may not be completely at risk from crop damage, commercial operations can have the means to eradicate crop foragers from their area, as has been the case with baboons in some areas of South Africa and Zimbabwe (Lamarque et al. 2008).

Few studies have been published on the extent of wildlife damage to commercial farms (Decker and Brown 1982, Wywialowski 1994, Jonker et al. 1998, Bal et al. 2011) and even fewer on the extent of primate damage (Engeman et al. 2010). Engeman et al. (2010) estimated the economic costs of primate damage to commercial farms in Puerto Rico at a total of \$1.13-1.46 million USD per year, likely a conservative estimate. Conover (1998) estimated that agricultural producers in the United States alone sustain an annual loss of \$2 billion USD to wildlife. Crop losses on commercial farms are thus substantial and are likely to increase without significant action. Furthermore, while the extent of primate damage on commercial farms is poorly understood, even fewer studies have been published on primate crop-foraging behavior on these farms.

Knowledge of primate crop-foraging patterns is essential for the planning, implementation, and monitoring of mitigation techniques. As such, this should include a detailed understanding of the underlying factors, patterns, and processes associated with crop foraging (Hill 2017*b*). A number of crop-foraging variables have been shown to affect the intensity of crop damage caused by primates, including crop-foraging frequency, duration, and the number of individuals involved (Hill 2000, Wallace 2010). In turn, these variables have been shown to be affected by several factors, such as species involved, interspecific interactions, season, and time of day (Maples et al. 1976, Kavanagh 1980, Linkie et al. 2007, Warren 2008).

Competitive and interspecific interactions, such as predator-prey interactions, affect primate foraging patterns (Willems and Hill 2009) and therefore may also influence crop-foraging activity. As seasons change and natural food availability fluctuates, so too does wildlife crop damage; usually a reduction in natural food availability leads to an increase in crop damage (Sekhar 1998, Hockings et al. 2009, Nyirenda et al. 2011, Mikich and Liebsch 2014). This pattern is not universal among primates, however, with many reports of severe primate crop damage taking place irrespective of surrounding natural food availability (Naughton-Treves et al. 1998, Riley 2007, Riley and Priston 2010, Cancelliere et al. 2018).

Primate crop foraging has been reported to reflect general circadian activity patterns for primates (Altmann and Altmann 1970, Hill et al. 2004), with activity peaking early and late while reducing during the middle of the day (Saj et al. 1999, Wallace 2010). Again, however, the pattern is not universal; Campbell-Smith et al. (2011) reported Sumatran orangutans (*Pongo abelii*) foraged on cultivated fruits mostly in the afternoons and evenings when farmers had left the farms to return to their village for the night, while chimpanzees (*Pan troglodytes*) have even been recorded foraging within crops during the night, despite normally being strictly diurnal (Krief et al. 2014).

We studied chacma baboon (*Papio ursinus*; baboon) and vervet monkey (*Chlorocebus pygerythrus*; vervet) crop-foraging behavior on a commercial farm in South Africa to determine the extent of crop damage caused by these species. We were also interested in describing the factors that influenced baboon and vervet crop foraging (i.e., interspecific interactions, natural food availability, time of day, and nature of field visits) to inform commercial farmers about strategies that could be used to mitigate potential conflicts.



800 Km

200 400



Figure 2. (A) Chacma baboon (*Papio ursinus*) exiting a crop field and (B) vervet monkeys (*Chlorocebus pygerythrus*) in a crop field, both on a commercial farm in Limpopo, South Africa, 2013 (*photos courtesy of L. Findlay*).

Study area

We conducted our case study in 2013 on a 564-ha commercial farm located within the Blouberg District Municipality, situated in the far north of the Limpopo Province, South Africa (22°40′08.05″S, 28°46′47.73″E; Figure 1). The climate is semi-arid with warm, wet sum-

mers (October to March) and cooler, dry winters (April to September). Temperatures ranged from an average daily minimum of 13°C in June and July to an average daily maximum of 33°C in November, with a mean annual temperature of 25°C. Annual rainfall was 650 mm, most of which fell during the summer months; the area is prone to frequent drought, and the Mogalakwena River is the only perennial river (Grwambi et al. 2006).

The commercial farm we studied lies within the Limpopo Sweet Bushveld vegetation type, which is defined as plains, sometimes undulating or irregular, traversed by several tributaries and comprised of short open woodland in distributed thickets of blue thorn (Vachellia erubescens), black thorn (Senegalia mellifera), and sicklebush (Dichrostachys cinerea; Mucina and Rutherford 2006). Limpopo is an important area for crop production, producing more tomatoes (Solanum lycopersicum) than any other province and 20% of South Africa's potatoes (S. tuberosum; Tibane 2015). Other locally grown crops included onions (Allium cepa), dry beans (Phaseolus spp.), and tobacco (Nicotiana spp.), as well as a variety of pumpkins and squashes (Cucurbita spp.), melons (Citrullus lanatus and Cucumis melo), and citrus fruits (*Citrus* spp.).

Crop foraging by wildlife occurs on commercial farms within the Blouberg District, and crop losses may be underestimated by farmers (Findlay 2016). Crop-foraging species in the area include chacma baboon (Figure 2A), vervet monkey (Figure 2B), common warthog (Phacochoerus africanus), bushpig (Potamochoerus larvatu), Cape porcupine (Hystrix africaeaustralis), bushbuck (Tragelaphus sylvaticus), and helmeted guineafowl (Numida meleagris). Most farmers in the area employ field guards 7 days a week from dawn to dusk to protect their crops, most often unarmed women who chase, shout, and sometimes throw stones at wildlife entering crop fields. Many farmers also revert to lethal methods of control, such as shooting (Findlay 2016).

We selected a farm in northern Blouberg to conduct our preliminary study because of the farmers' willingness to participate and known problems with crop losses to primates. The farm was typical to the area in terms of size, crops grown, and farming and mitigation activities. The study farm was 564 ha in size, with

Figure 3. Observation hide from which behavioral data collection took place on a commercial farm in Limpopo, South Africa, 2013.

80 ha for crops. Remaining land was used for game farming of a variety of antelope species including sable (*Hippotragus niger*), greater kudu (*Tragelaphus strepsicero*), and blue wildebeest (*Connochaetes taurinus*). Crops have been produced on this farm for 14 years and wild primates that forage on crops have been subject to shooting for many years (commercial farmer, personal communication).

Within the farm, we selected a 1-ha field as our primary study area. The farmer reported that this field received more damage than other fields from crop-foraging wildlife. The crop edge was separated from the bushveld by a small cattle fence approximately 10 m from the field. The farmer planted butternut squash (*Cucurbita moschata*) on January 29, 2013 and harvested for the first time at the end of June and for the last time on August 20, 2013.

Methods

We recorded our field observations using binoculars from a blind placed in a corner of the squash field closest to natural bushveld (Figure 3). Although we focused our data collection on 1 field, we could see from this vantage point if baboons or vervets were visiting the other crop fields. We recorded our observations from May 7 to August 20, 2013 for 5 days per week from dawn until dusk. We separated days into 2 sessions, morning (0600-1200 hours) and afternoon (1200–1800 hours), swapping observers between sessions to avoid researcher fatigue. Each time a baboon or vervet was heard or seen from our observation point, we recorded data on a voice recorder (Olympus IEC/JIS LR03, Southend-on-Sea, United Kingdom) and continued recording every minute until the animals could no longer be seen or heard. We recorded the number of individuals observed and their locations (Altmann 1974).

We distinguished field visits—when baboons or vervets were seen or heard by the observer and were therefore nearby the crop fieldsand crop-foraging events-when baboons or vervets actually entered the crop field. Thus, a field visit could contain any number of cropforaging events, including none at all, and several field visits could occur on the same day. We calculated field visits from the time a baboon or vervet was first seen or heard by the observer until the last individual was seen or heard for that visit. More than 1 hour had to pass with no sightings or vocalizations heard for a subsequent sighting to be classified as a new field visit (Tobler et al. 2008). We assumed that after a period of 1 hour with no detection that the group had moved away. If we only detected baboons or vervets audibly (and therefore did not see them in any of the crop fields) and the visit lasted <30 minutes we did not count it as a field visit. For these instances, we assumed that the group or individual was passing by the crop fields rather than entering them.

Crop-foraging attempts started when a baboon or vervet approached the small livestock fence next to the crops and became a successful cropforaging event if and when the first individual entered the crop field; these events ended when the last individual exited the field. If an individual exited the field but re-entered the crops within 1 minute without crossing the fence, we considered the event to be continuous, but the time spent outside the field was subtracted from the total time spent within crops (if there were no other individuals within the field during this time). We recorded instances of simultaneous foraging by >1 species as separate crop-foraging events for those species.

We video-recorded (Canon Legria HFR506, Uxbridge, United Kingdom) and coded all foraging events. We recorded the primate species, time when first individual entered the field, the number of additional individuals that entered the field, time when the last individual exited the field, and number of butternut squash each individual was carrying on exit. From these data, we extracted the duration of each foraging event, number of individuals involved in each

event, and number of items removed during each event. The amount of crop loss was estimated from observations of individuals carrying squash out of the field. We estimated the economic costs of baboon and vervet crop damage by using the market value of butternut squash at the time of harvest (R35-40 ZAR [South African rand] per bag, averaging 8 butternuts per bag) and extrapolated the number of items removed from the field to include days we did not observe. We did not survey the area where animals were observed for damage within the field, as cropforaging events often occurred one after another and we did not want our presence within the field to affect subsequent behavior. We were therefore unable to assess the additional damage to the crop such as plants or squash bitten into and left in the field. Our measure of damage was therefore an underestimate.

We used the normalized difference vegetation index (NDVI; downloaded from Global Land Cover Facility 2015) as a measure of natural habitat productivity. As an index of plant photosynthetic activity, NDVI ranges between -1 and 1, with a higher NDVI indicating greener vegetation present and therefore more availability of natural forage (Jiang et al. 2006). Values of NDVI for dense vegetation generally range from 0.3-0.8; values <0.3 indicate shrub and grassland, and values <0.2 tend to denote bare soils (Earth Observatory 2000). While NDVI does not measure primate food (particularly fruit) availability directly, macaques inhabiting forests with higher NDVI fed more on fruits and seeds and had greater dietary diversity (Tsuji et al. 2015), and local foraging and range use by vervet monkeys could be determined by local NDVI (Willems et al. 2009). Crop foraging by elephants (Loxodonta spp.) entering neighboring farmland has also been associated with a decline in NDVI within Gorongosa National Park (Branco et al. 2019). While fruits and tubers, preferred natural foods of baboons (Hill and Dunbar 2002), generally mature after seasonal peaks in photosynthetic activity and thus NDVI, leaves and grasses, which NDVI does measure, are an important fallback food for baboons (Hill and Dunbar 2002). Declines in NDVI are thus likely to reflect a general decline in habitat productivity with concomitant declines in food availability. Members of the public can also gain access to NDVI, and as such it is a measure of natural habitat productivity that is accessible to the farmer.

We conducted all data collection under the guidelines and approval of Durham University's Animal Welfare Ethical Review Board (formerly Life Sciences Ethical Review Process Committee) and a permit issued from the Limpopo Department of Economic Development, Environment and Tourism. Data collection methods adhered to the American Society of Primatologists Principles for the Ethical Treatment of Non-Human Primates.

Data analyses

We examined the difference in the number of squash removed from the field (hereafter referred to as damage) between the 2 species using a Wilcoxon rank sum test. We used a multiple regression (function glmmADMB), with a negative binomial distribution to account for overdispersion, to determine whether baboon presence had an effect on crop damage caused by vervets and whether NDVI and session (morning or afternoon) had an effect on crop damage caused by each species. We included the number of observation hours per day as an offset and day as a random variable. We used a segmented regression to determine when significant changes in crop damage took place across values of NDVI.

We used chi-square tests to determine which species was more likely to crop forage when visiting the fields, whether single- or multicrop foraging events were more likely, and whether the 2 species differed in how often they were involved in single- or multi-crop foraging event field visits. We conducted a Spearman's rank correlation to test the relationship between field visit durations and the number of crop-foraging events. We performed all statistical analyses using R (R Core Team 2014) and the following packages within R: lme4 (Bates et al. 2015), car (Fox and Weisberg 2011), glmmADMB (Fournier et al. 2012), and segmented (Muggeo 2003). Where incomplete data occurred, data points were excluded depending on variables being tested. For example, events where the time of first entry was missed but all individuals were recorded were removed when examining duration of events but not when examining the number of individuals involved in events.



Figure 4. Number of butternut squash (*Cucurbita moschata*) removed per day by chacma baboons (*Papio ursinus*) and vervet monkeys (*Chlorocebus pygerythrus*) from a 1-ha crop field on a commercial crop farm in Limpopo, South Africa, May to August 2013.

Results

We conducted 699 hours and 58 minutes of observation hours for baboons and 713 hours and 50 minutes for vervets. We removed some observation time from the analysis for baboons because of incomplete data collection, resulting, for example, from video camera storage running out before crop-foraging events ended.

We recorded 202 field visits (baboon = 110, vervet = 92) involving 643 crop-foraging attempts (baboon = 344, vervet = 299) and 506 successful crop-foraging events (baboon = 287, vervet = 219). This amounted to 353 hours and 22 minutes that primates spent in field visits (baboon = 249 hours and 15 minutes, vervet = 104 hours and 7 minutes; 35.6% and 14.6% of observation time, respectively) and 16 hours and 3 minutes within the crops (baboon = 6 hours and 54 minutes, vervet = 9 hours and 9 minutes; 1.7% and 5.3% of their field visit time, respectively).

We observed a minimum of 2,368 individual entries into the field (baboon = 1,939, vervet = 429) during foraging events. Of these entries, at least 102 (baboon = 64, vervet = 38) were the same individual entering the field more than once in the same foraging event. Individual foraging events involved between 1 and 63 baboons (mean = 7.01 ± 0.56) and between 1 and 18 vervets (mean = 2.12 ± 0.15).

We observed a minimum of 1,794 butternut squash being removed from the field (baboon = 1,526, vervet = 268) over 106 days of observation. This equated to an economic loss caused by baboons and vervets of R14,219–16,250 ZAR (\$1,402-1,603 USD at 2013 exchange rates; baboon = R12,132–13,865 ZAR, \$1,197–1,367 USD; vervet = R2,087–2,385 ZAR, \$205–235 USD). Baboons caused almost 6 times more damage than vervets across the observation period (*W* = 3,023.5, *P* = 0.003; Figure 4).

Natural habitat productivity, indicated by NDVI, decreased over the observation period. This decrease had an effect on crop damage caused by baboons with a 6-fold increase in squash removed by the end of the season (β = -20.382, SE = 6.154, *P* = 0.001; Figure 5A). Habitat productivity did not have an effect on vervet crop damage (β = 4.021, SE = 4.255, *P* = 0.340). Segmented regression revealed that baboon damage increased significantly below an NDVI value of 0.315 (Davies test, *P* = 0.029; Figure 5B). Vervet damage decreased at an NDVI value of 0.330 (Davies test, *P* = 0.851; Figure 5C).

The presence of baboons, as measured by their field visit duration per session, decreased vervet crop damage (β = -0.00007, SE = 0.00002, *P* = 0.010; Figure 6). Presence of baboons, however, did not affect vervet field visit duration (β = -0.00005, SE = 0.00004, *P* = 0.202).

Time of day influenced crop damage caused by baboons, with baboons causing 3 times more crop damage during morning sessions than afternoon sessions (β = -1.067, SE = 0.355, *P* = 0.003; Figure 7). In contrast, time of day did not appear to affect the intensity of crop damage caused by vervets (β = -0.199, SE = 0.331, *P* = 0.550).

Forty-three percent of primate field visits (baboon = 48.6%, vervet = 34.0%) did not involve crop foraging at all (Figure 8A). Vervets were 15% more likely to crop forage when they visited than baboons (chi-square: χ_1^2 = 4.490, *P* = 0.034). Of the visits that involved crop foraging, 69% more baboon visits involved multiple crop-foraging events rather than a single event, while 34% more vervet visits involved multiple events (chi-square: baboon $-\chi_1^2$ = 14.222, *P* ≤ 0.001; vervet $-\chi_1^2$ = 17.515, *P* ≤ 0.001; Figure 8B). There was no difference between species in how often they were involved in single- or multi-

Baboon and vervet crop-foraging behavior • Findlay and Hill



Figure 5. (A) Relationship between number of butternut squash (*Cucurbita moschata*) removed by chacma baboons (*Papio ursinus*) per session and normalized difference vegetation index (NDVI). The dashed line shows the linear regression; dotted lines show the confidence intervals for the slope estimate. (B) Number of butternut squash removed by chacma baboons per session across NDVI displaying break points at which amount of damage changes with changing NDVI and (C) number of butternut squash removed by vervet monkeys (*Chlorocebus pygerythrus*) per session across NDVI displaying break points at which amount of damage changes with changing NDVI. Note that the x-axis has been reversed on all figures to display the temporal pattern of an increase in crop foraging over the study period (May to August 2013), all from a commercial crop farm in Limpopo, South Africa.



Figure 6. Relationship between number of butternut squash (*Cucurbita moschata*) removed by vervet monkeys (*Chlorocebus pygerythrus*) and the presence of chacma baboons (*Papio ursinus*) at the observation field (field visit duration) per session on a commercial crop farm in Limpopo, South Africa, May to August 2013. The dashed line shows the linear regression; dotted lines show the confidence intervals for the slope estimate.



Figure 7. Effect of time of day on the number of butternut squash (Cucurbita moschata) removed by chacma baboons (*Papio ursinus*) on a commercial crop farm in Limpopo, South Africa, May to August 2013.



Figure 8. (A) Number of chacma baboon (*Papio ursinus*) and vervet monkey (*Chlorocebus pygerythrus*) field visits that did and did not involve crop-foraging events (CFEs) and (B) number of baboon and vervet monkey field visits that involved single- and multi-crop foraging events on a commercial crop farm in Limpopo, South Africa, May to August 2013.

crop foraging event field visits (chi-square test, $\chi^2_1 = 0.078$, P = 0.781). We found a strong positive correlation between the duration of field visits and the number of crop-foraging events, with an additional crop-foraging event occurring every 43.4 minutes of field visit duration ($r_s = 0.653$, n = 240, $P \le 0.001$, mean visit duration = 1 hour and 28 minutes), that was true for both species independently (baboon: $r_s = 0.737$, n = 140, $P \le 0.001$; vervet: rs = 0.635, n = 100, $P \le 0.001$).

Discussion

Baboons and vervets were regularly observed foraging on crops on a commercial farm in Limpopo Province, South Africa, with baboons causing more damage than vervets. Habitat productivity and time of day had different effects on the crop-foraging patterns of the 2 species, with baboons foraging more later in the season when natural productivity was low and more often in the morning. The presence of baboons had a deterrent effect on vervet crop-foraging behavior. Although only from a single crop field in a single season, and being limited in our ability to make generalizations, our results provide a starting point for other researchers to build up a knowledge base of primate foraging behavior on commercial farms and for commercial farmers to consider potential mitigation strategies. Our recommendations are thus specific to our local context and further site and species-specific information would need to be collected to consider applying more broadly.

Crop losses were estimated at an economic loss of \$1,402–1,603 USD from 1 ha of crops during a single season. We collected these data from a field chosen based on reports that it suffered the most crop-foraging activity; hence, not all fields may experience such extensive damage. While all fields experienced some level of wildlife crop damage, the amount of damage varied widely from field to field (Findlay 2016). Our estimate for the study field is likely to be conservative, however, given that we used the number of items removed from the field as a proxy for damage and so did not count damaged items left within the fields. Furthermore, these losses occurred with a paid field guard in place, who is effective at reducing crop losses (Findlay and Hill 2020). Nevertheless, if an alternative deterrent eliminated the need for field guards, this salary, as well as the savings from reduced crop damage, could be put toward the cost of the deterrent.

Baboons caused more damage to the farmer's crops than vervets, corroborating local farmer opinion (Findlay 2016) as well as numerous other studies that report baboons to cause more crop loss than any other primate species (Hill 1997, Kagoro-Rugunda 2004, Mackenzie and Ahabyona 2012, Mackenzie et al. 2015). Interestingly, baboon presence reduced vervet damage. Baboons are known predators of

vervet monkeys (DeVore and Washburn 1963, Altmann and Altmann 1970, Hausfater 1976, Willems and Hill 2009), and vervets may also be spatially supplanted by baboons, especially in open habitats (Struhsaker 1967). We observed vervets leaving the crop field in response to the arrival of baboons on numerous occasions. Although the presence of baboons reduced the number of butternut squash removed by vervets, it did not reduce the amount of time vervets spent around the field (i.e., their field visit durations). Instead, vervets retreated to natural habitat at the field edge, a safe location from which they could continue their field visits and monitor for crop-foraging opportunities. As baboons increased the time they spent foraging within crop fields toward the end of the season, there may have been very few chances for vervets to forage, leading to the observed decrease in vervet damage.

Crop depletion on the edge of the fields may account for the difference. In Uganda, vervets travelled up to 55 m into crop fields, while baboons ventured up to 110 m (Wallace 2010); crops may thus be depleted within vervet foraging range later in the season. Farmers are also aware of the increased risk of crop damage by wildlife at the edges of fields and consequently harvest these areas first (Findlay 2016), thereby depleting the crops within vervet but not baboon crop-foraging ranges. The observed crop field was harvested for the first time at the end of June. Further research is needed to determine which of these factors-baboon presence, edge depletion, or farmer harvesting—has the most influence on vervet crop foraging.

One potential implication of these findings is that successfully deterring baboons could lead to a subsequent increase in vervet foraging, particularly because vervets are often not detected by guards (Findlay and Hill 2020). Vervets have been reported to cause high amounts of crop damage (Saj et al. 2001, Sillero-Zubiri and Switzer 2001, Lee and Priston 2005, Ango et al. 2016), and many farmers in the study area perceived vervets to be a significant problem by damaging crops (Findlay 2016). Mitigation strategies thus need to account for both baboons and vervets.

Crop loss caused by baboons increased throughout the season as habitat productivity of surrounding areas decreased, as described in other crop-foraging studies (Naughton-Treves et al. 1998, Kagoro-Rugunda 2004, Strum 2010, Krief et al. 2014). Crop foraging by baboons intensified when NDVI declined below 0.32. Values of ≥ 0.3 indicate dense vegetation, while <0.3 indicates shrub and grassland (Earth Observatory 2000), suggesting that as NDVI values decline to 0.3, so too does the suitability of natural vegetation as an adequate foraging resource. Taking into account that crops were protected by a field guard (Findlay and Hill 2020), it appears that when habitat productivity drops below a certain threshold, the benefits of crop-foraging increase and so the risk of a field guard without a weapon becomes less of a deterrent. This strongly indicates that the reduction in habitat productivity and concomitant availability of natural food sources stimulates crop foraging by baboons. Vervets did not follow the same pattern and generally showed no differences in crop foraging as habitat productivity decreased, although this may be better explained by other factors than a lack of response to a reduction in habitat productivity. To reduce crop losses, farmers could monitor local NDVI values and increase deterrent efforts when values drop below 0.32; when using field guards, this could be done by increasing the number of guards present.

While crop loss caused by vervets did not appear to change between morning and afternoon sessions, baboons caused more damage in the morning. Schweitzer et al. (2017) recorded a peak in chacma baboon crop foraging in Zimbabwe between 0800 and 1000 hours and concluded that feeding on high nutrient crops in the morning allowed the baboons to spend more time socializing and resting during the rest of the day. Priston (2005) found crop foraging by Buton macaques (Macaca ochreata brunnescens) in southeast Sulawesi, Indonesia to be more frequent in the mornings and suggested this was because of the need to find food upon waking. In contrast, Wallace (2010) found primates in Uganda foraged on crops more between noon and sunset than between sunrise and noon. Wallace (2010) suggested these differences in the diurnal pattern of crop foraging were tied to local factors. The baboons that visited our study field regularly used a sleeping site approximately 300 m from the crop field and could quickly access the field upon waking without traveling a significant distance. That vervets did not follow the same daily pattern could suggest that vervet sleeping sites were further from the field (and the baboons), although their precise location was unknown.

Baboons and vervets spent around half of our observation time in field visits. Baboons have been shown to employ a "sit and wait" strategy at the edge of crop fields while they look for opportunities to forage within crops (Walton et al., in press). Although the time they spent actually foraging within crops was much less, there was a positive correlation between field visit time and number of crop-foraging events (i.e., baboons and vervets are more likely to forage within crops the longer they spend close to the fields).

When baboons and vervets did enter crops during these visits, they were more likely to enter multiple times rather than just once, as was also found for baboons and vervets on subsistence farms in Uganda (Wallace 2010). There was no difference between the species in whether they were involved in multi- or single-crop foraging event visits, despite guards responding to many more baboon events compared with vervets (Findlay 2016, Findlay and Hill 2020). Our data therefore suggests that as it is currently performed, chasing has no effect on whether baboons or vervets return to the crop field to undertake subsequent foraging. If guards could decrease the likelihood of baboons and vervets returning to the field, crop losses could be reduced. Crop damage may be reduced by field guards herding baboons and vervets away from crop fields altogether (see also Walton et al., in press), rather than just to the edge of the crop field as they currently do, or by increasing the perceived risk of the guards.

Management implications

The crop loss we estimated in the study field was significant, despite field guards being present to protect crops from foraging animals. The losses warranted the additional time, labor, and money to deter the animals responsible. Given the potential losses to primates on commercial crop farms being substantial, further research into more expensive deterrent methods, such as electric fencing, may reveal that such investment is cost-effective in the longer term. However, we suggest that implementing less expensive options using strategies currently available may better mitigate crop losses to baboons and vervets. This may be achieved by: paying attention to local NDVI values and implementing extra deterrents when values fall below 0.32; increasing perceived risk of field guards through the use of weapons, such as bear bangers (Kaplan 2013), or switching field guards from female to male employees, or adding male guards when risks are greatest, as primates are often less intimidated by women than men (Asquith 1989, Mackenzie et al. 2015); and more active guarding involving herding animals away from crops altogether rather than just to the edge of fields.

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Literature cited

- Altmann, J. 1974. Observational study of behavior: sampling methods. Behaviour 49:227–267.
- Altmann, S. A., and J. Altmann. 1970. Baboon ecology: African field research. University of Chicago Press, Chicago, Illinois, USA.
- Anand, S., V. V. Binoy, and S. Radhakrishna. 2018. The monkey is not always a God: attitudinal differences toward crop-raiding macaques and why it matters for conflict mitigation. Ambio 47:711–720.
- Anand, S., and S. Radhakrishna. 2017. Investigating trends in human–wildlife conflict: is conflict escalation real or imagined? Journal of Asia-Pacific Biodiversity 10:154–161.
- Ango, T. G., L. Borjeson, and F. Senbeta. 2016. Crop raiding by wild mammals in Ethiopia: impacts on the livelihoods of smallholders in an agriculture-forest mosaic landscape. Oryx 51:527–537.

Asquith, P. 1989. Provisioning and the study of

free ranging primates: history, effects, and prospects. American Journal of Physical Anthropology 32:129–158.

- Bal, P., C. D. Nath, K. M. Nanaya, C. G. Kushalappa, and C. Garcia. 2011. Elephants also like coffee: trends and drivers of human–elephant conflicts in coffee agroforestry landscapes of Kodagu, Western Ghats, India. Environmental Management 47:789–801.
- Bates, D., M. Mäechler, B. Bolker, and S. Walker. 2015. Fitting linear mixed-effects models using Ime4. Journal of Statistical Software 67(1):1–48.
- Branco, P. S., J. A. Merkle, R. M. Pringle, J. Pansu,
 A. B. Potter, A. Reynolds, M. Stalmans, and R.
 A. Long. 2019. Determinants of elephant foraging behaviour in a coupled human-natural system: is brown the new green? Journal of Animal Ecology 88:780–792.
- Campbell-Smith, G., M. Campbell-Smith, I. Singleton, and M. Linkie. 2011. Raiders of the lost bark: orangutan foraging strategies in a degraded landscape. PLOS ONE 6(6): e20962.
- Campbell-Smith, G., H. V. P. Simanjorang, N. Leader-Williams, and M. Linkie. 2010. Local attitudes and perceptions toward crop-raiding by orangutans (*Pongo abelii*) and other nonhuman primates in northern Sumatra, Indonesia. American Journal of Primatology 72:866–876.
- Cancelliere, E. C., C. A. Chapman, D. Twinomugisha, and J. M. Rothman. 2018. The nutritional value of feeding on crops: diets of vervet monkeys in a humanized landscape. African Journal of Ecology 56:160–167.
- Conover, M. R. 1998. Perceptions of American agricultural producers about wildlife on their farms and ranches. Wildlife Society Bulletin 26:597–604.
- Decker, D. J., and T. L. Brown. 1982. Fruit growers' vs. other farmers' attitudes toward deer in New York. Wildlife Society Bulletin 10:150–155.
- DeVore, I., and S. L. Washburn. 1963. Baboon ecology and human evolution. Pages 335–367 in F. C. Howell and F. Bourlière, editors. African ecology and human evolution. Transaction Publishers, Chicago, Illinois, USA.
- Earth Observatory. 2000. Measuring Vegetation. Earth Observatory, National Aeronautics and Space Administration, Washington, D.C., USA, <http://earthobservatory.nasa.gov/Features/ MeasuringVegetation/>. Accessed March 16, 2016.
- Engeman, R. M., J. E. Laborde, B. U. Constantin,

S. A. Shwiff, P. Hall, A. Duffiney, and F. Luciano. 2010. The economic impacts to commercial farms from invasive monkeys in Puerto Rico. Crop Protection 29:401–405.

- Fehlmann, G., M. J. O'Riain, C. Kerr-Smith, S. Hailes, A. Luckman, E. L. C. Shepard, and A. J. King. 2017a. Extreme behavioural shifts by baboons exploiting risky, resource-rich, human-modified environments. Scientific Reports 7:15057.
- Fehlmann, G., M. J. O'Riain, and A. J. King. 2017b. Adaptive space use by baboons (*Papio ursinus*) in response to management interventions in a human-changed landscape. Animal Conservation 20:101–109.
- Findlay, L. J. 2016. Human–primate conflict: an interdisciplinary evaluation of wildlife crop raiding on commercial crop farms in Limpopo Province, South Africa. Dissertation, Durham University, Durham, United Kingdom.
- Findlay, L. J., and R. A. Hill. 2020. Field guarding as a crop protection method: preliminary implications for improving field guarding. Human– Wildlife Interactions 14:519–530.
- Fournier, D. A., H. J. Skaug, J. Ancheta, J. Ianelli, A. Magnusson, M. N. Maunder, A. Nielsen, and J. Sibert. 2012. Using automatic differentiation for statistical inference of highly parameterized complex nonlinear models. Optimization Methods and Software 27:233–249.
- Fox, J., and S. Weisberg. 2011. An R companion to applied regression. Second edition. Sage, Thousand Oaks, California, USA.
- Global Land Cover Facility. 2015. Normalised difference vegetation index. Global Land Cover Facility, University of Maryland, College Park, Maryland, USA, http://glcf.umd.edu/data/ndvi/. Accessed August 31, 2015.
- Grwambi, B., U. Kolanisi, N. Maine, K. Mphahlele, N. Raidimi, and K. Ramaifo. 2006. Livelihoods in the rural areas of Blouberg Municipality (Gemarke & Early Dawn villages), Limpopo Province, South Africa. Working Document Series 129. International Centre for Development Oriented Research in Agriculture, Wageningen, The Netherlands; Limpopo Department of Agriculture, Polokwane, South Africa; and Agricultural Research Council Sustainable Rural Livelihoods Division, Pretoria, South Africa.
- Hausfater, G. 1976. Predatory behavior of yellow baboons. Behaviour 56:44–68.
- Hill, C. M. 1997. Crop-raiding by wild vertebrates:

the farmer's perspective in an agricultural community in western Uganda. International Journal of Pest Management 43:77–84.

- Hill, C. M. 1998. Conflicting attitudes towards elephants around the Budongo Forest Reserve, Uganda. Environmental Conservation 25:244– 250.
- Hill, C. M. 2000. Conflict of interest between people and baboons: crop raiding in Uganda. International Journal of Pest Management 21:299–315.
- Hill, C. M. 2002. Primate conservation and local communities—ethical issues and debates. American Anthropologist 104:1184–1194.
- Hill, C. M. 2005. People, crops and primates: a conflict of interests. Pages 40–59 in J. D. Paterson, editor. Primate commensalism and conflict. American Society of Primatologists, Norman, Oklahoma, USA.
- Hill, C. M. 2017*a*. Crop raiding. *In* A. Fuentes, editor. The international encyclopedia of primatology. John Wiley & Sons, Inc, Hoboken, New Jersey, USA.
- Hill, C. M. 2017b. Primate crop feeding behavior, crop protection, and conservation. International Journal of Primatology 38:385–400.
- Hill, C. M. 2018. Crop foraging, crop losses, and crop raiding. Annual Review of Anthropology 47:377–394.
- Hill, C. M., and A. D. Webber. 2010. Perceptions of nonhuman primates in human–wildlife conflict scenarios. American Journal of Primatology 72:919–924.
- Hill, R. A., and R. I. M. Dunbar. 2002. Climatic determinants of diet and foraging behaviour in baboons. Evolutionary Ecology 16:579–593.
- Hill, R. A., T. Weingrill, L. Barrett, and S. P. Henzi. 2004. Indices of environmental temperatures for primates in open habitats. Primates 45:7–13.
- Hockings, K. J., J. R. Anderson, and T. Matsuzawa. 2009. Use of wild and cultivated foods by chimpanzees at Bossou, Republic of Guinea: feeding dynamics in a human-influenced environment. American Journal of Primatology 71:636–646.
- Jiang, Z., A. R. Huete, J. Chen, Y. Chen, J. Li, G. Yan, and X. Zhang. 2006. Analysis of NDVI and scaled difference vegetation index retrievals of vegetation fraction. Remote Sensing of Environment 101:366–378.
- Jonker, S. A., J. A. Parkhurst, R. Field, and T. K. Fuller. 1998. Black bear depredation on agricultural commodities in Massachusetts. Wildlife Society Bulletin 26:318–324.

- Kagoro-Rugunda, G. 2004. Crop raiding around Lake Mburo National Park, Uganda. African Journal of Ecology 42:32–41.
- Kaplan, B. 2013. In pursuit of a panacea: mitigating human–baboon conflict in the Cape Peninsula, South Africa. Dissertation, University of Cape Town, Cape Town, South Africa.
- Kavanagh, M. 1980. Invasion of the forest by an African savannah monkey: behavioural adaptations. Behaviour 73:238–260.
- Krief, S., M. Cibot, S. Bortolamiol, A. Seguya, J. M. Krief, and S. Masi. 2014. Wild chimpanzees on the edge: nocturnal activities in croplands. PLOS ONE 9(10):e109925.
- Lamarque, F., J. Anderson, P. Chardonnet, R. Fergusson, M. Lagrange, Y. Osei-Owusu, L. Bakker, U. Belemsobgo, B. Beytell, H. Boulet, B. Soto, and P. Tabi Tako-Eta. 2008. Human–wildlife conflict in Africa—an overview of causes, consequences and management strategies. International Foundation for the Conservation of Wildlife, and Food and Agriculture Organisation of the United Nations, Rome, Italy.
- Lee, P. C., and N. E. C. Priston. 2005. Human attitudes to primates: perceptions of pests, conflict and consequences for primate conservation. Pages 1–23 *in* J. D. Patterson and J. Wallis, editors. Commensalism and conflict: the humanprimate interface. American Society of Primatologists, Norman, Oklahoma, USA.
- Ling, T. S. 2016. Mapping the current and past distribution of Asian elephants (*Elephas maximus*) and human–elephant conflict (HEC) in humanoccupied landscapes of Peninsular Malaysia. Thesis, University of Nottingham, Nottingham, United Kingdom.
- Linkie, M., Y. Dinata, A. Nofrianto, and N. Leader-Williams. 2007. Patterns and perceptions of wildlife crop raiding in and around Kerinci Seblat National Park, Sumatra. Animal Conservation 10:127–135.
- Mackenzie, C. A., and P. Ahabyona. 2012. Elephants in the garden: financial and social costs of crop raiding. Ecological Economics 75:72–82.
- Mackenzie, C. A., R. R. Sengupta, and R. Kaoser. 2015. Chasing baboons or attending class: protected areas and childhood education in Uganda. Environmental Conservation 42:373–383.
- MacLarnon, A. M., V. Sommer, A. S. Goffe, J. P. Higham, E. Lodge, P. Tkaczynski, and C. Ross. 2015. Assessing adaptability and reactive scope: introducing a new measure and illus-

trating its use through a case study of environmental stress in forest-living baboons. General and Comparative Endocrinology 215:10–24.

- Maples, W. R., M. K. Maples, W. F. Greenhood, and M. L. Walek. 1976. Adaptations of cropraiding baboons in Kenya. American Journal of Physical Anthropology 45:309–316.
- Mason, J. R. 1998. Mammal repellents: options and considerations for development. Pages 324– 329 *in* Proceedings of the Eighteenth Vertebrate Pest Conference, Costa Mesa, California, USA.
- McLennan, M. R., and C. M. Hill. 2012. Troublesome neighbours: changing attitudes towards chimpanzees (*Pan troglodytes*) in a humandominated landscape in Uganda. Journal for Nature Conservation 20:219–227.
- Mikich, S. B., and D. Liebsch. 2014. Damage to forest plantations by tufted capuchins (*Sapajus nigritus*): too many monkeys or not enough fruits? Forest Ecology and Management 314:9–16.
- Mucina, L., and M. C. Rutherford. 2006. The vegetation of South Africa, Lesotho and Swaziland. South African National Biodiversity Institute, Pretoria, South Africa.
- Muggeo, V. M. 2003. Estimating regression models with unknown break-points. Statistics in Medicine 22:3055–3071.
- Nahallage, C. A. D., M. A. Huffman, N. Kuruppu, and T. Weerasingha. 2008. Diurnal primates in Sri Lanka and people's perception of them. Primate Conservation 23:81–87.
- Naughton-Treves, L. 1997. Farming the forest edge: vulnerable places and people around Kibale National Park, Uganda. Geographical Review 87:27–46.
- Naughton-Treves, L., A. Treves, C. Chapman, and R. Wrangham. 1998. Temporal patterns of crop-raiding by primates: linking food availability in croplands and adjacent forest. Journal of Applied Ecology 35:596–606.
- Nyirenda, V. R., W. C. Chansa, W. J. Myburgh, and B. K. Reilly. 2011. Wildlife crop depredation in the Luangwa Valley, eastern Zambia. Journal of Ecology and the Natural Environment 3:481–491.
- Priston, N. E. C. 2005. Crop-raiding by *Macaca* ochreata brunnescens in Sulawesi: reality, perceptions and outcomes for conservation. Dissertation, University of Cambridge, Cambridge, United Kingdom.
- R Core Team. 2014. R: a language and environment for statistical computing. R Foundation

for Statistical Computing, Vienna, Austria.

- Riley, E. P. 2007. The human–macaque interface: conservation implications of current and future overlap and conflict in Lore Lindu National Park, Sulawesi, Indonesia. American Anthropologist 109:473–484.
- Riley, E. P., and N. E. C. Priston. 2010. Macaques in farms and folklore: exploring the human– nonhuman primate interface in Sulawesi, Indonesia. American Journal of Primatology 71:1–7.
- Saj, T. L., P. Sicotte, and J. D. Paterson. 1999. Influence of human food consumption on the time budget of vervets. International Journal of Primatology 20:974–977.
- Saj, T. L., P. Sicotte, and J. D. Paterson. 2001. The conflict between vervet monkeys and farmers at the forest edge in Entebbe, Uganda. African Journal of Ecology 39:195–199.
- Schweitzer, C., T. Gaillard, C. Guerbois, H. Fritz, and O. Petit. 2017. Participant profiling and pattern of crop-foraging in chacma baboons (*Papio hamadryas ursinus*) in Zimbabwe: why does investigating age–sex classes matter? International Journal of Primatology 38:207–223.
- Sekhar, N. U. 1998. Crop and livestock depredation caused by wild animals in protected areas: the case of Sariska Tiger Reserve, Rajasthan, India. Environmental Conservation 25:160–171.
- Siex, K. S., and T. T. Struhsaker. 1999. Colobus monkeys and coconuts: a study of perceived human–wildlife conflicts. Journal of Applied Ecology 36:1009–1020.
- Sillero-Zubiri, C., and D. Switzer. 2001. Crop raiding primates: searching for alternative, humane ways to resolve conflict with farmers in Africa. People and Wildlife Initiative, Wildlife Conservation Research Unit, Oxford University, Oxford, United Kingdom.
- Starin, E. D. 1989. Threats to the monkeys of the Gambia. Oryx 23:208–214.
- Struhsaker, T. T. 1967. Ecology of vervet monkeys (*Cercopithecus aethiops*) in the Masai-Amboseli Game Reserve, Kenya. Ecology 48:891–904.
- Strum, S. C. 2010. The development of primate raiding: implications for management and conservation. International Journal of Primatology 31:133–156.
- Tchamba, M. 1996. History and present status of the human/elephant conflict in the Waza-Logone region, Cameroon, West Africa. Biological Conservation 75:35–41.

- Tibane, E. 2015. South Africa yearbook 2014/15. Department of Government Communication and Information Systems, Pretoria, South Africa.
- Tobler, M. W., S. E. Carrillo-Percastegui, R. Leite Pitman, R. Mares, and G. Powell. 2008. An evaluation of camera traps for inventorying large- and medium-sized terrestrial rainforest mammals. Animal Conservation 11:169–178.
- Tsuji, Y., T. Y. Ito, K. Wada, and K. Watanabe. 2015. Spatial patterns in the diet of the Japanese macaque *Macaca fuscata* and their environmental determinants. Mammal Review 45:227–238.
- Tweheyo, M., C. M. Hill, and J. Obua. 2005. Patterns of crop raiding by primates around the Budongo Forest Reserve, Uganda. Wildlife Biology 11:237–247.
- Wallace, G. E. 2010. Monkeys in maize: primate crop-raiding behaviour and developing on-farm techniques to mitigate human–wildlife conflict. Dissertation, Oxford Brookes University, Oxford, United Kingdom.
- Walton, B. J., L. J. Findlay, and R. A. Hill. 2020. Insights into short- and long-term crop-foraging strategies in a chacma baboon (*Papio ursinus*) from GPS and accelerometer data. Ecology and Evolution 11:990–1001.
- Warren, Y. 2008. Crop-raiding baboons (*Papio anubis*) and defensive farmers: a West African perspective. West African Journal of Applied Ecology 14:1–11.
- Waters, S. S. 2015. Crop-raiding Baird's tapir provoke diverse reactions from subsistence farmers in Belize. Conservation 24:8–10.
- Webber, A. D. 2006. Primate crop raiding in Uganda: actual and perceived risks around Budongo Forest Reserve. Dissertation, Oxford Brookes University, Oxford, United Kingdom.
- Willems, E. P., R. A. Barton, and R. A. Hill. 2009. Remotely sensed productivity, regional home range selection, and local range use by an omnivorous primate. Behavioral Ecology 20:985–992.
- Willems, E. P., and R. A. Hill. 2009. Predatorspecific landscapes of fear and resource distribution: effects on spatial range use. Ecology 90:546–555.
- Wywialowski, A. P. 1994. Agricultural producers' perceptions of wildlife-caused losses. Wildlife Society Bulletin 22:370–382.

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