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Participant Profiling and Pattern of Crop-Foraging in Chacma Baboons (*Papio hamadryas ursinus*) in Zimbabwe: Why Does Investigating Age–Sex Classes Matter?

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Abstract Transformation and loss of natural habitat to urbanization and agriculture provide new opportunities for primates to feed on anthropogenic food sources. Currently, mitigation strategies fail to target the individuals responsible for initiating and maintaining this behavior. As primates mainly forage on crops in groups, we investigate the crop-foraging behavior of a group of 40 chacma baboons in Zimbabwe from the perspective of collective movements, i.e., when a group of animals move together in the same direction, thus resulting in a change of location. We collected data on 110 crop-foraging events during 35 days in March–April 2014. We recorded baboon movement and behavior with a camcorder and obtained further information through video analysis. Most crop-foraging events involved less than 20% of the troop and lasted less than 3 min. Although crop-foraging parties were composed of all age–sex classes, adult females and particularly adult males initiated most crop-foraging events and made direct movements (without stopping on the road) more often than nonadult participants.

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Baboons made up to five successive attempts to crop forage in a single crop-foraging event. Neither the number of participants nor the success of the crop-foraging events increased over the successive attempts. Finally, crop-foraging events were more successful and more frequent in unguarded areas than in guarded areas. These results suggest that group members are highly synchronized and that crop-foraging is based on a collective decision such as classical foraging movements. In addition, the short duration of the crop-foraging events might prevent detection of baboons by farmers. The more frequent initiation of crop-foraging by adults compared to nonadults might be explained by greater energetic needs or a greater tendency of adults to take risks. These preliminary data can help inform long-term strategies for farmers to reduce crop losses to baboons, as guarding helps reduce damage but does not prevent it.

Keywords Coordination · Crop-raiding · Danger · Decision-making · Foraging strategy

Introduction

Loss of natural habitat due to urbanization and agriculture provides primates with opportunities to feed on anthropogenic food sources. This expansion of the anthropogenic landscape provides easy access to high-energy food, leading to improved growth and reproduction, and allows primates to allocate more time to socializing (Forthman-Quick and Demment 1988; Strum 2010; Warren 2008). However, crop-foraging generates negative consequences for long-term coexistence between humans and nonhuman primates, through negative perceptions of wildlife by humans, threats to infrastructures, and human safety hazards (Hill 2005; Regmi *et al.* 2013; Sillero-Zubiri and Switzer 2001; see also Hockings and McLennan 2012). In this context, primates are likely to be victims of harassment, injury, or even death during confrontations with local people (Strum 1994, 2010).

Because crop-foraging implies a trade-off between energy needs and risk taking (Strum 2010), primates may decide collectively when and where to forage on crops, and which individuals will participate (some group members apparently choose not to forage on crops, even if others do; Wallace and Hill 2012; Warren 2008). Primates forage on crops mainly in groups (Hockings and McLennan 2012; Hockings *et al.* 2015; Naughton-Treves 1997; Wallace and Hill 2012). This collective behavior is likely to follow the patterns found in other spontaneous collective movements, which are based on distributed leadership where all group members can initiate movements and be successfully followed (Boinski and Garber 2000; Byrne 1981, 2000; King *et al.* 2011; Rhine and Westlund 1981; Rowell 1969; Strandburg-Peshkin *et al.* 2015; Stueckle and Zinner 2008; Sueur 2011). Group size affects the appearance of leadership, organization of individuals, and communication during group movements in baboons (Sueur 2011). It is thus likely to provide relevant information about collective decision processes involved in crop-foraging events and whether they are like those during natural foraging. The smaller group size expected for crop-foraging parties (Strum 2010; Wallace and Hill 2012) may bias the probability of socializing and may result only from shared individual characteristics at a given time (energetic needs, food specialization, risk prone, etc.).

Coordination between group members may also be a key factor in the collective decision to forage on crops. Coordination can be achieved through the display of predeparture behaviors (Guinea baboons, *Papio papio*: Byrne 1981; Hamadryas baboons, *Papio hamadryas*: Kummer 1968; yellow baboons, *Papio cynocephalus*: Norton 1986; rhesus and Tonkean macaques, *Macaca mulatta* and *Macaca tonkeana*: Sueur and Petit 2008) or by mimetic processes during joining, which may be driven by social relationships (Jacobs *et al.* 2011; King *et al.* 2011; Meunier *et al.* 2006; Sueur 2011; Sueur *et al.* 2009).

The efficacy of management strategies will differ considerably depending on whether animals behave collectively or independently. Traditional methods sometimes include the use of scents or fences but mainly farmers guard the fields to scare and chase crop foragers, and in extreme situations hunt them. Specific individuals may be solely responsible for foraging on crops or bringing other group members to do so. If this is the case, mitigation strategies should focus on these individuals. However, current management strategies do not target the individuals responsible for initiating and maintaining the behavior (Hill 2015, 2017; Sillero-Zubiri and Switzer 2001).

We aimed to identify whether crop-foraging events result from a collective decision or whether attraction to crops is the main factor responsible for the emergence of collective output, without coordination between group members (King and Cowlishaw 2009; Petit and Bon 2010). We assessed crop-foraging events in baboons (*Papio hamadryas ursinus*) at the edge of an anthropogenic habitat on the northern periphery of Hwange National Park in Zimbabwe, where primarily elephants (*Loxodonta africana*) and baboons are responsible for crop loss in subsistence farming systems (Guerbois *et al.* 2012). We hypothesize that crop-foraging will have underlying mechanisms similar to those of spontaneous collective movements with a synchronization of group members. Baboon crop-foraging is a foraging strategy (Strum 2010), but occurs under more dangerous conditions than other foraging (Forthman-Quick and Demment 1988), so we predict that crop-foraging events will be concentrated in time (Strum 1994, 2010; Swedell 2011), and involve few group members (Wallace and Hill 2012; Warren 2008). We also test the influence of crop type on crop-foraging. Based on studies of collective movements, we predict that adult individuals initiate more crop-foraging events than other age–sex classes, but that the age–sex class of the initiator should not influence the number of participants. Moreover, we predict that adult males initiate crop-foraging events more frequently than other age–sex classes because crop-foraging is risky and that adult females and nonadult individuals behave more cautiously with more aborted attempts at crop-foraging than adult males. In addition, if baboons are aware that this foraging strategy is risky, we predict a higher number of attempts and successful crop-foraging events in unguarded crop areas than in guarded ones.

Methods

Study Area

The study area is located at the periphery of Hwange National Park (14,500 km^2) in Zimbabwe, at the interface between two protected areas (a forestry area and Hwange National Park) and communal lands. The communal area is bordered to the south by the

Main Camp area, to the east by Sikumi Forest (1200 km^2), to the north by Hwange Rural District (Matabeleland North) and to the southeast by the town of Dete (long. 26°87′E, lat. 18°62′S; Fig. 1). The area is unfenced; the western boundary between Sikumi Forest and the communal area comprises a tarmac road whereas no specific infrastructure delineates the northern boundary. This configuration, where cultivated areas are close to the forest edge and render human food easily available, favors crop-foraging (Sillero-Zubiri and Switzer 2001; Warren *et al.* 2011) and a shift from foraging on natural resources to foraging on crops (Strum 2010; Warren 2008). This mosaic of landscapes highlights the complexity of the social-ecological systems that integrate a variety of stakeholders (i.e., farmers, researchers, wildlife managers, and conservationists) and attitudes toward wildlife.

Fig. 1 (a) Land cover in the study area on the periphery of Hwange National Park, Zimbabwe captured on Google Earth and calibrated with field measurements. **(b)** Chacma baboons (*Papio hamadrays ursinus*) crossing back over the road after foraging on crops with children running after them (April 2014). Fields are on the right side of the picture and the forest is on the left side.

Baboons are listed as a Problem Animal in the Parks and Wild Life Act (PWL Act 1991) under the Eighth schedule, section 80. According to SI 59 and 60 of the PWL Act, community members are not allowed to kill "problem animals" themselves (although people often take the law into their own hands). However, according to SI 77 of the PWL Act, the minister may authorize a conservation committee (such as the Rural District Council, Parks, Forestry Commission) to reduce, i.e., kill, animals that cause excessive damage or nuisance. Hence, both people and wildlife bear the costs of their interactions along the borders of protected areas, with negative consequences for both the survival of baboons and the well-being of subsistence farmers.

The study area is classified as agro-ecological regions IV and V (Mugandani *et al.* 2012), characterized by low-fertility soils (mostly Kalahari sands) and erratic low annual rainfall (606 mm, interannual CV = 25%). This part of Sikumi Forest between protected and communal lands (Fig. 1) is composed of miombo woodland dominated by *Brachystegia spiciformis*, with patches of *Colophospermum mopane*. In the communal area, subsistence crops include maize (*Zea mays*), sorghum (*Sorghum bicolor*), and pearl millet (*Pennisetum glaucum*) (Guerbois *et al.* 2012). Farmers generally start planting crops in November and harvest between April and May. We collected data in March and April 2014 when most crops were mature. The timing of crop planting, growth, and maturity was synchronized across the farms we studied and adjoining farms. The three types of crop were not equally distributed across the 28 fields adjacent to the forestry in the study area. Maize was the main crop, with 79% of the fields ($N = 22$), 21% for millet ($N = 6$), and 18% for sorghum ($N = 5$). Four fields were planted with both maize and sorghum (one of these included three types of crop).

Data Collection

T. Gaillard and a local Zimbabwean ranger, working with the forestry and skilled in English as well as the local languages, carried out fieldwork from the beginning of March to early April 2014. As agreed with all farmers before starting the fieldwork, observers did not intervene during crop-foraging events or in baboon–farmer interactions. We collected data with the consent and support of the local stakeholders. We carried out observations from a research car parked along the road, on the forestry side. We used this strategy to avoid being perceived as a threat by the baboons. Farmers were on foot and those in charge of guarding usually stood on the other side of the road. Furthermore, baboons were accustomed to cars in this area and did not seem to be affected by the presence of observers. When baboons moved from one field to another, observers followed them with the car respecting a minimum distance of ca. 20 m from the closest individuals. We started observations at sunrise (06:00 h), as soon as crop-foraging events were likely to occur, and ended them at 14:00 h because we never observed crop-foraging events after 14:00 h in preliminary field observations.

Study Group and Identification

The study group of baboons lived at the border between the forest and rural lands. We determined group composition and identified age–sex classes based on direct observations using binoculars (×12 to ×50 lenses). We categorized individuals into four age–sex classes: adult males and adult females (full size), subadults (not fully grown,

beyond juvenile in size, unidentified sex), and juveniles (smaller than subadults, maintaining close proximity to adults, unidentified sex) (from Wallace and Hill 2012). The study group included 40 individuals, made up of 6 adult males, 14 adult females, 10 subadults, and 10 juveniles.

Definitions

We termed any observation of one or more baboons moving toward crop fields, in prominent positions overlooking crop fields, or of baboons foraging on crops a crop-foraging event (Wallace and Hill 2012). We classified crop-foraging events as successful or unsuccessful depending on their outcome (Warren 2008). A successful crop-foraging event started when the first individual (the initiator) exited the forest boundary—delimited by the trees—and ended when the last individual exited the field. It did not imply that the baboons consumed or interacted with crops in the field because our observation procedure did not allow us to access this information. We considered all departing movements in the same direction as the initiator and within 5 min of the initiation to be a following movement. We considered individuals performing these behaviors within 20 m or more as followers (as defined in Sueur and Petit 2008). When baboons terminated an attempted crop-foraging event before entering the crop area, we defined this as an unsuccessful crop-foraging event. We considered successive movements in a 20-min window as a single crop-foraging event divided into successive attempts (defined by preliminary field observations). We ordered the successive attempts by their time of occurrence for subsequent analysis.

Monitoring Crop-Foraging Events

We collected data using continuous sampling (Altmann 1974). We split fieldwork tasks between the two observers. The ranger recorded the baboons' movement and behavior with a camcorder (Panasonic HX-WA2). Meanwhile, T. Gaillard identified the initiator and followers, and recorded information using a voice recorder (ZicPlay Microkey). We started the film as soon as an individual moved beyond the forest border. For each crop-foraging event, we collected the following information: 1) date and time; 2) GPS position of the field and type of crop; 3) outcome (successful/not successful); 4) identity of the initiator and the first two followers, i.e., age–sex class (when possible); and 5) presence or absence of the farmer, identity of the farmer, and any actions taken toward baboons. We considered both guarding by humans (farmers or children) and dogs as active guarding, i.e., attempts to prevent baboons from entering the field. People used various techniques to stop baboons from crop-foraging, including shouting, throwing rocks, and running after baboons. We did not consider children playing on the road (see Fig. 1b) or nearby the field as guarding. Since they viewed baboons from the car, observers generally could not see whether the monkeys consumed or interacted with crops in the field and thus the overall impact of crop-foraging was difficult to assess. However, crop loss is related to the number of participants and the length of the crop-foraging events (Wallace and Hill 2012). We obtained further information through video analysis. We used a VLC player to measure the length of crop-foraging events and duration of pauses before entering the crop area, and to record the age–sex classes of the baboons, party size, and behaviors (glances, pauses on the

road). We also distinguished direct crop-foraging events (baboons crossed the road directly and entered the field) from indirect crop-foraging events (baboons paused in the road before continuing toward the field and eventually entering it).

Statistical Analysis

We performed all statistical analyses and created figures with R 3.2 (R Core Team 2016). When required, we log-transformed the variables to achieve or approximate a normal distribution. When the transformation still did not result in a normal distribution, we used nonparametric tests. First, we assessed the difference in the distribution of the crop-foraging events over the 06:00–14:00 h observation time between the four age–sex classes or the three types of crop (maize, sorghum, and pearl millet) using mixed-effect linear models with the farm as a random variable. We used chi-square tests to determine whether the number of crop-foraging events differed between three categories of group sizes (fewer than 10 individuals, 10–20 individuals, and more than 20 individuals) and whether the number of initiators differed among the four age–sex classes. When the number of observations was too low to perform chi-square tests, we calculated P-values using the Monte Carlo simulation. We assessed the relationship between group size and crop-foraging event duration using Pearson's correlation tests. Then, we tested whether adult males were more prone to initiate crop-foraging events than adult females and nonadult individuals. To this end, we used similar mixed-effect linear models with the farm as a random variable to test the effect of the initiator's age–sex class on the number of participants, crop-foraging event duration, and type of strategy (direct or indirect crop-foraging event). To avoid type I error inflation, we used Bonferroni's adjustment for multiple *post-hoc* pairwise comparisons. Finally, we assessed what made a successful crop-foraging event and tested the effect of guarding on success. We compared the number of participants involved in successful and unsuccessful crop-foraging events using a Mann–Whitney U test. We also investigated the potential factors influencing success (guarding, observation time, age–sex class of the initiator or type of crop) using mixed-effect linear models with the farm as a random variable.

Results

Pattern of Crop Foraging

We recorded 110 crop-foraging events during 35 daily observation sessions of 5–7 h each. We removed two events from subsequent analyses because we could not determine whether they were successful or not. Crop-foraging events occurred only between 06:00 h and 14:00 h with a peak between 08:00 h and 10:00 h (Shapiro–Wilk test: $W = 0.95$; $P < 0.001$; Fig. 2), regardless of the type of crop (mixed-effects linear model: $\chi^2_3 = 3.14$, $P = 0.21$). The median group size of the crop-foraging events was three individuals (25th–75th percentiles: 1–11 individuals). Most crop-foraging events (70%) involved fewer than 10 individuals, 18% were by 10–20 individuals, and 12% involved more than 20 individuals (chi-square test: $\chi^2_2 = 56.5$, $P < 0.001$). The median duration of the crop-foraging events was 165 s (25th–75th percentiles: 35–352 s). There was no

significant relationship between group size and crop-foraging event duration (Pearson's correlation: $r = 0.14$, 95% CI = -0.18, 0.44, $P = 0.39$).

In 57% of crop-foraging events, baboons crossed the road directly and entered the field (direct crop-foraging event), while in the other 43%, baboons paused on the road before continuing toward the field and eventually entering it (indirect crop-foraging event). The mean pause duration was 17.8 s and pause duration ranged from 3 to 160 s (see Fig. 4b). In 14% of the crop-foraging events an individual crossed the forest boundary but then turned back toward the forest, without attempting to enter the field. These baboons glanced at their conspecifics and paused on the road. Crop-foraging events preceded by these abandoned attempts were significantly less frequent than crop-foraging events without abandoned attempts (chi-square test: $\chi^2_1 = 51.9$, $P < 0.001$).

The Crop Foragers

Crop-foraging parties involved all age–sex classes but initiation was not distributed equally among the four age–sex classes (chi-square test: $\chi^2_3 = 28.8$, $P < 0.001$). Females and males initiated crop-foraging events more often than subadults and juveniles (Fig. 3). In addition, the distribution of observed initiations among the age–sex classes differed significantly from initiations expected based on group composition (6 adult males, 14 adult females, 10 subadults, and 10 juveniles; chi-square test: $\chi^2_3 = 19.15$, $P < 0.001$). Adult males initiated more crop-foraging events than expected, whereas juveniles initiated fewer crop-foraging events than expected ($\chi^2_1 = 8.28$,
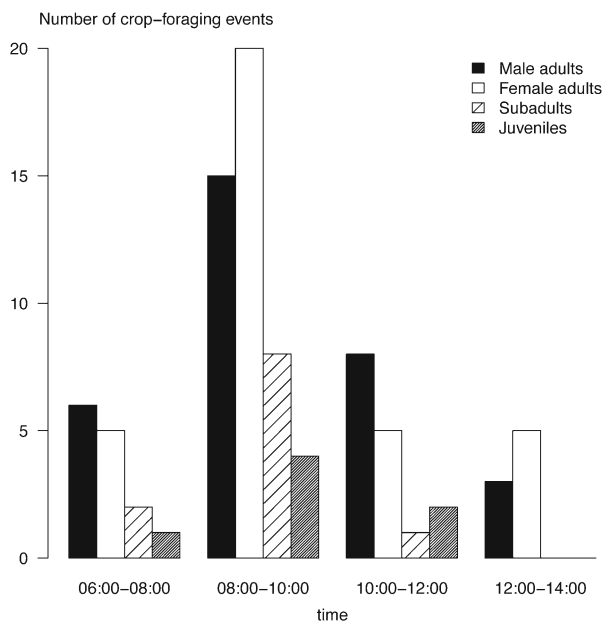
Fig. 2 The number of crop-foraging events initiated by different age–sex classes over the 06:00–14:00 h observation period in a group of chacma baboons on the periphery of Hwange National Park, Zimbabwe, in April 2014.

$P = 0.004$ and $\chi^2_1 = 7.19$, $P = 0.007$, respectively). We found no significant difference for adult females ($\chi^2_1 = 0.42$, $P = 0.51$) or subadults ($\chi^2_1 = 3.26$, $P = 0.07$).

The daily timing of crop foraging did not differ with the age–sex class of the initiator (mixed-effects linear model: $\chi^2_3 = 0.41$, $P = 0.94$; Fig. 2). Similarly, the age–sex class of the initiator did not significantly explain the number of followers (mixed-effects linear model: $\chi^2_3 = 2.23$, $P = 0.52$), the age–sex class of the first or second followers (Monte Carlo simulations: $\chi^2 = 8.71$, $P = 0.52$ and $\chi^2 = 10.4$, $P = 0.34$, respectively) or crop-foraging event duration (mixed-effects linear model: $\chi^2_3 = 2.47$, $P = 0.48$).

We found an effect of the initiator's age–sex class on the type of strategy used (mixed-effects linear model: $\chi^2_3 = 30.7$, $P < 0.001$). While adults initiated both direct and indirect crop-foraging events, subadults and juveniles only initiated indirect crop-foraging events (Fig. 4a), with the longest pauses occurring when juveniles were the initiators (Fig. 4b). In contrast, the number of crop-foraging events preceded by an abandoned attempt did not vary significantly with age–sex class (generalized linear model: $\chi^2_3 = 0.85$, $P = 0.077$).

What Made a Successful Crop-Foraging Event?

Seventy-three percent of crop-foraging events were successful (79 successful crop-foraging events vs. 29 unsuccessful crop-foraging events). Guarding had a significant influence on whether a crop-foraging event was successful (generalized linear mixed-effects model: $\chi^2_1 = 13.05$, $P < 0.001$). Crop-foraging events were more successful in unguarded areas (77 successful vs. 20 failed crop-foraging events; Monte Carlo
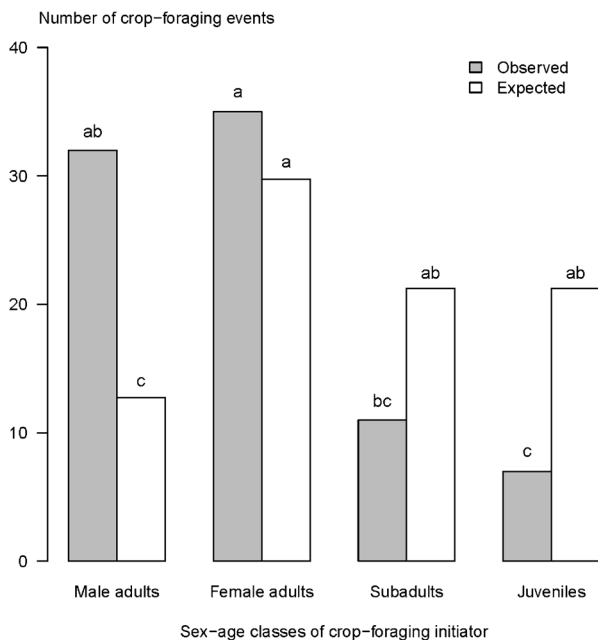
Fig. 3 The observed and expected distribution of age–sex classes of a group of chacma baboons that initiated crop-foraging events on the periphery of Hwange National Park, Zimbabwe, in April 2014. Letters indicate significant differences between the categories ($P < 0.05$, pairwise comparisons with Bonferroni's adjustment).

a Number of crop–foraging events

b Latency to enter the crop area (s)


Sex−age classes of the initiator
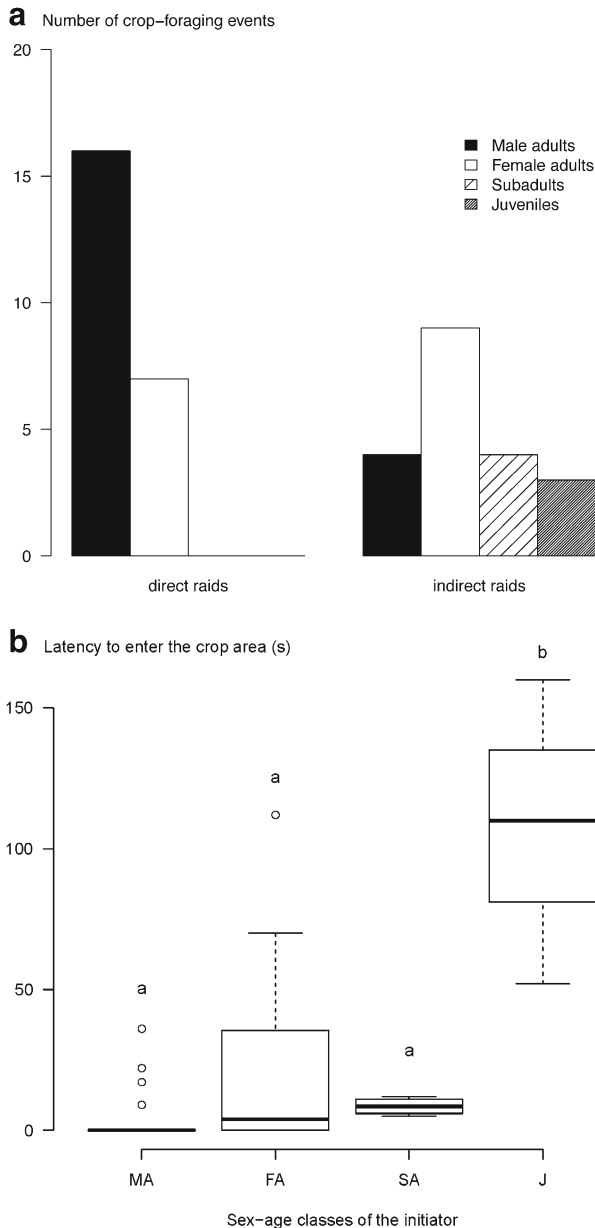
Fig. 4 **(a)** The number of direct and indirect crop-foraging events initiated by four age–sex classes (MA = male adults; FA = female adults; SA = subadults; J = juveniles) of a group of chacma baboons on the periphery of Hwange National Park, Zimbabwe in April 2014, and **(b)** their latency to enter the crop area. Box plots show medians inside 25th–75th percentile boxes and whiskers to 1.5 interquartile range. Letters indicate significant differences between categories [Tukey's *post-hoc* tests (95% CI): MA vs. J: (−142.4; 63.4) FA vs. J: (46.9; 126.9) and SA vs. J: (−147.4; −50.2)].

simulation: $\chi^2 = 29.4$, $P = 0.001$), but this was not the case in guarded areas (2 successful vs. 9 failed crop-foraging events; $\chi^2 = 2.27$, $P = 0.22$) (Fig. 5). In

addition, successful crop-foraging events involved significantly more foragers compared to the unsuccessful ones (median, 25th–75th quartiles: 7, 2–16 individuals vs. 1, 1–2 individuals; Mann–Whitney U test: $U = 314$, $N_1 = 69$, $N_2 = 24$, $P < 0.001$). No other factor significantly influenced whether a crop-foraging event was successful (generalized linear mixed-effects model: time: $\chi^2_1 = 1.64$, $P = 0.20$; age–sex class of the initiator: $\chi^2_3 = 5.63$, $P = 0.13$; the type of crops: $\chi^2_2 = 1.75$, $P = 0.42$). We observed a maximum of five successive attempts for a single crop-foraging event in a given field within 20 min. However, we used crop-foraging events only with a maximum of three attempts in statistical analyses because successive crop-foraging events with four or five attempts were too rare (one and two occurrences, respectively). Neither the number of participants nor the success of the crop-foraging events increases over successive attempts (linear mixed-effects model: $\chi^2_2 = 3.57$, $P = 0.17$ and Monte Carlo simulation: $\chi^2 = 1.68$, $P = 0.49$, respectively).

Discussion

With a frequency of 0.5 crop-foraging events per hour of observation, crop-foraging events are clearly a concern at the periphery of Hwange National Park. This rate is markedly lower than described for yellow baboons in Kenya (1.8 crop-foraging events per hour; Maples *et al.* 1976) but is more frequent than for a group of olive baboons in Nigeria (0.08 crop-foraging events per hour; Warren 2008). It shows that current mitigation strategies are ineffective and the costs of not guarding fields are high. As predicted, when baboons entered fields on a given day, they concentrated this behavior
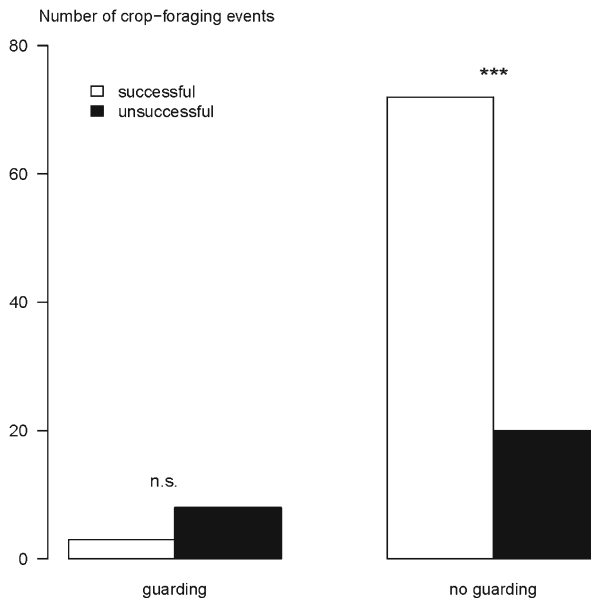
Fig. 5 The number of successful and unsuccessful crop-foraging events in guarded and unguarded crop areas. Data are for a group of chacma baboons on the periphery of Hwange National Park, Zimbabwe, in April 2014 (Monte Carlo simulation: ***$P = 0.001$; n.s.: $P > 0.05$).

in a period of a few hours. Feeding on high-nutrient crops only in the early morning would allow them to spend time socializing and resting rather than foraging during the rest of the day. Such influence of human-food consumption on baboon activity budgets has been demonstrated in previous studies (Forthman-Quick and Demment 1988; Strum 1994, 2010; Swedell 2011; Warren 2008) with an increase in the time devoted to resting and socializing in groups of crop-foragers compared to wild-foraging groups (Warren *et al.* 2011).

As predicted, crop-foraging events comprised a subset of the group, as in other baboons and primate species (Maples *et al.* 1976; Priston *et al.* 2012; Wallace and Hill 2012). Here, a maximum of 20% of the group members participated in crop-foraging events. A smaller crop-foraging party size than group size is apparently a general pattern in primates foraging on crops (Wallace and Hill 2012; Warren 2008). Foraging on crops in small groups is less conspicuous (Forthman-Quick and Demment 1988), less detectable by farmers and thus less risky for the monkeys. This observation is corroborated by the decrease in the number of vocalizations emitted by baboons while foraging on crops (Warren 2008) compared to the context of collective movements (Byrne 1981; Sueur 2011). Crop-foraging events were also short, as reported in other studies (Warren 2008; Warren *et al.* 2011), and the duration was irrespective of the age–sex class of the initiator. This supports Cowlishaw's (1997) suggestion that baboons adopt a time-minimizing strategy in areas with high predation pressure, to leave these areas as rapidly as possible (in the case of crop-foraging, the danger is represented by humans). However, an increase in crop-foraging duration with party size has been reported in several primate species, and for different group sizes (Wallace and Hill 2012). A similar pattern was also observed for foraging deer (*Capreolus capreolus*: Pays *et al.* 2012). However, we did not observe such a relationship in our study. This pattern might suggest that baboons are highly synchronized when entering and exiting the field, which may be favored by group cohesion before foraging on crops (Cowlishaw 1997). Such rapid phenomena might also reflect a consensus decision taken before moving that could be accelerated by mimetic processes during joining (Petit and Bon 2010). These two explanations are not mutually exclusive because consensus can result in better cohesion.

Although parties included all age–sex classes, as we predicted, adult females and males initiated crop-foraging events more often than subadults and juveniles. This result is similar to collective movements observed in wild-foraging groups of baboons where adults are more prone to depart first (Byrne 2000; King *et al.* 2011; Rowell 1969; Strandburg-Peshkin *et al.* 2015; Stueckle and Zinner 2008; Sueur 2011). Adults are more active in travel coordination and their decisions predominate, although subadult and younger group members also participate (Boinski and Garber 2000). In addition, and in accordance with our prediction, we found that males initiated crop-foraging events more frequently than expected by chance. Males are often reported as frequent initiators of collective movements in baboons (Byrne 2000; King *et al.* 2011; Rhine and Westlund 1981; Rowell 1969; Stueckle and Zinner 2008; Sueur 2011) and it has been proposed that their greater energetic needs might explain this higher propensity to perform initiations (Sueur 2011; Sueur *et al.* 2010). Nevertheless, in our study the crop-foraging party size did not differ with the age–sex class of the initiator. A similar lack of relationship between the number of followers and the identity of the initiator was reported for natural collective movements in baboons (King *et al.* 2011; Petit and Bon

2010; Stueckle and Zinner 2008; Sueur 2011). This pattern suggests that the decision is taken before initiation because the age–sex class of the initiator apparently does not influence the subsequent size of the following party.

Two different crop-foraging strategies took place during the crop-foraging events and might reflect the cautiousness of the initiator, as we have suggested. Only adults performed direct crop-foraging events without stopping on the road. Adults are more experienced than nonadults, which may explain these different strategies (Strum 2010). Besides experience, adults, especially males, might have a proactive behavioral type (fast explorer, bold, more active and aggressive; Réale *et al.* 2007; Sih *et al.* 2004) like chimpanzee males (*Pan troglodytes*) which are at the front of progressions while crossing roads (Cibot *et al.* 2015; Hockings *et al.* 2006) and act more impulsively (King et al. 2008a, b; Tamara *et al.* 2008). This suggestion is supported by the longer pauses displayed by juveniles while crossing the road compared to other age–sex classes. Interestingly, females performed as many direct crop-foraging events as indirect crop-foraging events. Females that performed indirect crop-foraging events may be those accompanied by infants who might be more cautious in this dangerous context (Wallace and Hill 2012). Female baboons with infants initiate group movements less often than females without infants (Stueckle and Zinner 2008; Sueur 2011). In contrast, lactating and pregnant females might be more prone to initiate crop-foraging events owing to their energetic needs. Individuals might be bolder and less cautious when starved (Luttberg and Sih 2010). In our study, lactating females and females with infants initiated fewer crop-foraging events (8 of 35), but they did not adopt one strategy over the other (four direct and four indirect crop-foraging events). However, we need more data to test this hypothesis about energetic drivers.

Fifteen crop-foraging events were preceded by an initiator (of any age–sex class) that crossed the forestry boundary but turned back toward the forest without entering the field, a cautious behavior that is expected in such risky conditions (Warren 2008). Before abandoning their crop-foraging attempt, these individuals glanced at their conspecifics and paused on the road. This checking behavior may allow the potential initiator to evaluate the risk of visiting the field and to abandon its crop-foraging attempt in case of danger. An alternative explanation is that these displays help to estimate the readiness of group members to follow, as described in other studies (Leca *et al.* 2003; Ramseyer *et al.* 2009). Where group members are reluctant to follow, the potential initiator might abandon its attempt. Moreover, a successful crop-foraging event involved a greater number of participants. These results suggest that crop-foraging is a collective phenomenon in which group members influence the initiator's behavior (Petit *et al.* 2009) rather than the sum of independent decisions. King and Cowlishaw (2009) suggested that such synchrony allows predator detection information to be shared quickly among group members thanks to coordinated antipredator scans. Neither the number of participants nor the success of crop-foraging events increased over successive attempts, suggesting that successive events in a given field within a short period of time might be independent and that distinct crop-foraging parties enter fields during the day. Such successive crop-foraging events have been reported in other primate species, such as vervet monkeys (*Chlorocebus aethipos*), red-tailed monkeys (*Cercopithecus ascanius schmidti*), and olive baboons (*Papio anubis*) (Wallace and Hill 2012). However, crop damage per crop-foraging event did not differ significantly between one event and successive events (Wallace and Hill 2012).

Additional work is needed to identify the participants of successive crop-foraging events to investigate this further.

Together, our results suggest that the decision-making processes that underlie crop-foraging are like collective decision making when moving in other environments, with a higher bias toward adult males for initiating crop-foraging compared to other movements, probably owing to the danger that an anthropogenic area represents. The specific risky context of crop-foraging could explain the switch from a totally shared consensus decision-making process to a partially shared process, as suggested by Petit and Bon (2010). The baboons could thus be seen as classical foragers that exploit the surrounding available food, i.e., crops, depending on collective foraging strategies. This supports the need to avoid use of a negative term, i.e., crop-raiding, for this collective behavior (Strum 2010) as well as for other primates (Hill 2015, 2017).

Finally, as we predicted, crop-foraging events were more successful and more frequent in unguarded areas. In guarded areas, we found differences in the number of successful and unsuccessful crop-foraging events, and that the guarding strategy was not sufficient to deter all foraging events. These findings confirm that guarding can be used to reduce damage but not to prevent them (Spagnoletti *et al.* 2016; Wallace and Hill 2012; Warren 2008). Baboons can sit for hours, waiting for farmers to leave the farm, before foraging on crops (Strum 1994). Mitigation strategies require us to understand the ecological flexibility of species (Hockings and McLennan 2012) and the factors and mechanisms involved in the shift from natural to crop foraging (Strum 2010). Individual identification of animals involved will provide information about whether the same individuals join the parties, forage on crops from one season to another, and have common characteristics (behavioral, physiological, or social) promoting crop-foraging. The complete chain of costs and benefits should differ based on dominance, physiological traits (lactating or breeding females, first reproduction or not, energetic needs, stress, etc.), sex, or affiliation of each individual (Strum 2010). More efficient mitigation strategies may thus target these specific individuals or traits. For instance, adults, including potentially lactating females, initiated most crop-foraging events, suggesting that energetic needs may be the motivation for foraging on crops. This suggests that methods to decrease the palatability of crops would be useful, e.g., using alternative types of crops, synchronizing crop maturity, and high resource availability in forests or conditioned taste aversion (Forthman *et al.* 2005; Hockings and McLennan 2012), as would a large distance between the forest edge and crop fields (Spagnoletti *et al.* 2016). The larger involvement of adult males in initiating crop-foraging events may also result from a higher propensity to take risks. This suggests that management strategies should focus on increasing the risk of entering crop areas, for example, by collaborative guarding. An additional strategy to prevent crop-foraging may be to determine the individual and environmental factors that result in abandoning crop-foraging attempts. A deeper understanding of this collective behavior will be of help in proposing innovative management and conservation strategies. Finally, we obtained authorization from farmers to observe baboons without intervening by explaining that such data will help to understand what solutions could be applied. The next step will be to involve farmers in developing the management techniques because effective long-term strategies require a combination of approaches that consider wildlife behavior and increase local people's tolerance and secure their livelihoods (Hill 2015; Hill and Wallace 2012; Hockings and McLennan 2012).

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