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Less bins, less baboons: reducing access to anthropogenic food effectively decreases the urban foraging behavior of a troop of chacma baboons (*Papio hamadryas ursinus*) in a peri-urban area

Frédéric Mazué² · Chloé Guerbois^{1,3} · Hervé Fritz^{1,2} · Nancy Rebout⁴ · Odile Petit^{2,5}

Abstract

In South Africa, chacma baboons (*Papio hamadryas ursinus*) living near peri-urban areas may forage on anthropogenic food. Baboons have been recorded to damage crops, scatter waste from trash bins, and damage homes. A number of methods have been tested over the past 20 years to solve these problems, but none proved successful over the long-term or involved considerable costs. An efficient management system requires a detailed knowledge of how baboon troops proceed and organize during these urban foraging actions. This study examines the response of a troop of baboons to an experimental reduction of anthropogenic food sources in a peri-urban environment, the George campus of Nelson Mandela University (SA). We gradually suppressed access to waste food in trash cans, reducing the amount of anthropogenic food available. This change in food availability led baboons to modify their urban foraging strategy. They compensated for the lack of anthropogenic food by spending more time foraging on natural food and less time in urban areas. However, the troop still exploited wastefree areas during the experiment and even more when the conditions were normal again. Overall, these results show the ability of baboons to adapt to changes in anthropogenic food availability but also that they are highly dependent on this type of resource. Limiting its access is a mitigation strategy that humans must absolutely develop for reaching a high level of coexistence with baboons.

Keywords Urbanization · Human–wildlife coexistence · Non-human primates · Waste management · Behavioral flexibility

¹ Odile Petit odile.petit@cnrs.fr

² Sustainability Research Unit, Nelson Mandela University, George, South Africa

³ REHABS, CNRS-UCBL-NMU, International Research
Laboratory, Nelson Mandela University, George,
South Africa

⁴ FaunaStats, Schiltigheim, France

⁵ UMR PRC, CNRS, Université de Tours, 37380 Nouzilly,
France

Introduction

Coexistence between humans and wildlife in peri-urban areas (i.e., landscape interface between town and forest) is a global issue. With the constant expansion of the urban area surface throughout the world, human beings are increasingly encroaching on wildlife habitats, leading to a growing number of human–wildlife negative interactions (Distefano 2005; Redpath et al. 2014). The expansion of human activity has reduced the natural habitat and resources available for wildlife (Cowlshaw and Dunbar 2000; Mulder and Coppolillo 2005). Wild animals have therefore moved into anthropogenic areas, even during periods where natural food is available in their home range (Fehlmann et al. 2017a, b). This competition for resources causes a problem of coexistence between humans and wildlife (Dickman 2010), with significant ecological consequences (Cooper and Ginnett 2000; Ripple and Beschta 2007; Woodroffe et al. 2005) such as the decline or extinction of local animal populations (Tilson et al. 2004). In Africa, negative interactions often occur between humans and mammals when the latter forage on crops, livestock or in peri-urban and urban areas (Hill 1997)—especially when plantations are subsistence crops—causing problems of food security in certain areas (Hill 2000).

Anthropogenic food offers an easily accessible nutritive and highly digestible food resource for wildlife and is available in high quantities all year around (Duhem et al. 2008). The cognitive abilities, social cooperation, communication, agility, manual dexterity, and behavioral flexibility of non-human primates provide them with all the skills needed to access these food resources (Else 1991). Indeed, baboons are commonly reported to enter peri-urban areas to search for food, causing considerable damage every year (Cowlshaw and Dunbar 2000; Lee and Priston 2005). They are known to forage on crops and dumps, in waste bins, or inside houses (Hill 1997; Hoffman and O’Riain 2010). During these events, baboons can scatter waste from bins and may cause damage to homes to which they gain access. They also destroy rain gutters and break tiles to feed on the invertebrates living underneath. In South Africa, although protected by legislation (Western Cape Nature Conservation 2000), property damage and stress for local residents ultimately results in baboons being injured or killed through poisoning or gunshot wounds (Beamish and O’Riain 2014).

For more than 20 years, researchers have developed solutions to mitigate baboon food foraging based on studies that demonstrated the cognitive and behavioral abilities of the species (Henzi et al. 2009).

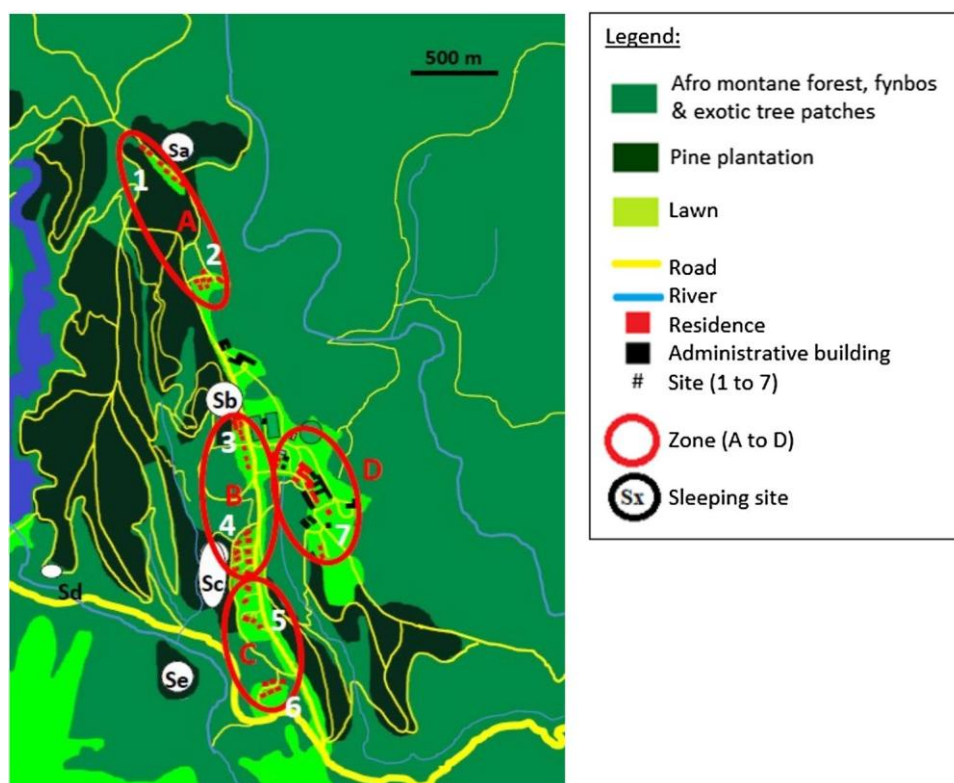
A variety of methods have been tested, including crop protection to limit access (Naughton-Treves 1997),

conditioned taste aversion and natural deterrents (Forthman et al. 2005; O’Brien and Hill 2018), translocation (Strum 2005), provisioning by creating a patch of food in a natural environment in order to reduce the presence of baboons in urban areas, the monitoring of baboon troops and the use of paintball guns to make them flee if they approach urban areas (van Doorn and O’Riain 2020), electric fences around residential areas (O’Riain and Hoffman 2010), reflective prisms (Kaplan and O’Riain 2015) or the culling of animals (Katsvanga et al. 2006). Although chasing the animals when they approach peri-urban areas (van Doorn and O’Riain 2020) or preventing access to homes with electric fences (O’Riain and Hoffman 2010) seem effective, these strategies are also expensive and not affordable to every city or city district. All the other methods failed to provide a long-term solution to the problem. One of the reasons for this failure is probably the lack of knowledge about how baboons operate when foraging in urban areas. As suggested by Schweitzer and colleagues, the development of an efficient management system requires a detailed knowledge of how the baboon troops proceed and organize themselves when foraging in urban areas (Schweitzer et al. 2017).

To understand the behavioral flexibility of baboons and the strategies they implement, one option is to set up experiments where food availability is manipulated. The current study aims to quantify the reactions of a troop of chacma baboons (*Papio hamadryas ursinus*) living at George campus of Nelson Mandela University (a peri-urban environment) when their source of anthropogenic food is partially reduced. In this experiment, we temporarily removed the waste from trash cans to reduce the amount of anthropogenic food available. We expected this sudden change in the distribution of resources in urban areas to modify the foraging strategy of baboons, possibly leading them to return to their natural habitats due to the scarcity of anthropogenic resources (Kaplan et al. 2011).

With this experiment of waste management, we expect that baboons will compensate for the lack of anthropogenic food by consuming natural food. In this context, a decrease should be observed in urban foraging time as well as the number of urban foraging events and participants, especially in the waste-free area. Alternatively, baboons could compensate for the scarcity of anthropogenic food in the waste-free area by increasing their foraging activity in other urban areas where waste is still available.

Fig. 1 Detailed map of the study area, including frequented area of the Madiba's troop in north of George, South Africa



Methods

Ethics statement

This research followed the American Society of Primatologists Code of Best Practices for Field Primatology and adhered to the legal requirements of South Africa in which the research was conducted.

Study site

The field study was conducted from February 1 to June 16, 2018, on the George campus of Nelson Mandela University (Nelson Mandela Boulevard, George Central, George, 6530 South Africa) (latitude: 33° 57'35.29 "S, longitude: 22° 31'54.61" E). The study area (approximately 8 km²) covers the entire zone exploited by the studied baboon troop all year round (Guerbois, personal communication). Main vegetation types include Afromontane Forest (endemic) and riverine vegetation along mountain streams, industrial pine plantations, and lawns used for sporting and leisure pursuits. Patches of native vegetation (fynbos) and exotic tree species are found around campus infrastructures such as roads, student residences, and campus buildings (Fig. 1).

Focal troop

The study troop of chacma baboons (*Papio hamadryas ursinus*) is called "Madiba's troop" and is one of the five

troops identified in the George peri-urban area (Pédarros et al. 2020). At the beginning of the study, the troop was comprised of 40 individuals, i.e., seven adult males (AM) and 11 adult females (AF) (full species-sex-specific size), eight subadults (S) (not fully grown, beyond infant development, frequently exhibiting independent behavior, unidentified sex), and 14 juveniles (J) (small and dependent, maintaining close proximity to adults, unidentified sex) (from Wallace and Hill 2012).

Two adult females gave birth during the study, thus increasing the size of the troop to 42 individuals at the end of the study, and one SA matured (seven AM, 12 AF, seven S, 14 J, and two infants). Only a few individuals were recognized by the observer (FM), so the study considered age and sex classes only. **Data collection**

Study area

By following the troop from early morning to late afternoon, we determined the area frequented by the troop (including urban and natural areas) and the location of their five resting sites (noted from Sa to Se in Fig. 1). The urban environment exploited by baboons was divided into several sites numbered from 1 to 7 based on the closeness and similarity of the infrastructures in terms of their location and function (Fig. 1). Sites 1 to 6 concerned residential buildings for staff and students except the 7th site, which was the center of the campus and included residences,

classrooms, and the cafeteria. The seven sites were split into four zones (A–D, Fig. 1). Zones A, B, and C had approximately the same number of habitations, while zone D was an area composed of a larger number of habitations (including residences and common areas). We grouped the different habitats into four categories: natural habitat (N) including the Afromontane Forest, the pine plantations, fynbos and exotic tree patches, edge (E) corresponding to the edge separating the natural environment from other environments, lawn (L) and urban area (U) corresponding to campus buildings.

Food supply reduction experiment

The food supply reduction experiment started on March 6 and ended on June 16, 2018 and was divided into four 3-week phases. No reduction of the food supply was carried out in the first (P1) and last phase (P4). During P2 and P3, from Monday to Saturday, a field assistant systematically emptied the waste cans in the waste-free zone to ensure that no food was accessible. The use of sports fields for tournaments caused the baboons to avoid the campus on Sundays (Mazué, personal observation). In the second phase (P2), waste was removed from zone D and in the third phase (P3), the waste-free area was enlarged to include zones D and B. Throughout the experiment, the baboon troop was monitored from sunrise to sunset, from Tuesday to Saturday (5 days a week for a total of 60 days), regardless of the climate conditions.

Procedure

Throughout the day, the troop alternated between several locations in the study area but always stayed together (within a 150-m radius). Any change in the troop position was recorded by an observer (FM) who followed the troop by bicycle and on foot when necessary. For each stopover (when the whole group stopped moving for a minimum of 5 min), the type of surrounding environment and the time of arrival and departure were recorded. In addition, the overall behavior of the troop (more than 70% of adult and subadult individuals) was recorded at the beginning of each stopover. Five behaviors were distinguished: Foraging (F), corresponding to any food-seeking activity for natural or anthropogenic items (including foraging when moving), Socializing (S), corresponding to all social interactions between members of the troop (including grooming, mating, conflict and play), Resting (R), corresponding to resting behavior, Exploration (E), corresponding to the exploration of an urban area without any urban foraging event (see definition below), and Travel (T), corresponding to the movement of the entire troop from point A to point B (without foraging). Any *urban foraging event* was recorded

with the behavior-dependent sampling method (Altmann 1974). An urban foraging event was defined as follows: baboons explore and/or empty a bin, try to open a window, a door or any other object that may contain anthropogenic food and sometimes enter houses. When the troop arrived at one of the seven urban sites, the observer noted the site number and the time at which an urban foraging event started (when an individual—the initiator—started any foraging action on a site) and ended (i.e., when the last baboon left the site) to calculate the duration of the event. In addition, the age–sex category of the initiator (MA, FA, S, J) was recorded as well as the number all participants. The number of waste bins explored and the number of windows and doors through which the baboons entered or attempted to enter the houses were recorded. Finally, other factors that could influence the progress of an urban foraging event were recorded, such as the presence of baboons foraging on the trees during the event, any human intervention (i.e., human action seeking to chase baboons from the urban area), and the number of people present on the site during the urban foraging.

Statistical analysis

All the statistical analyses were performed with R version 3.5.1 software with a significance threshold α set at 5% and the application conditions of each statistical test were verified prior to analysis.

For the first analysis, we wanted to know the influence of experiment on the time budget of the troop. The target variable was time budget allocation (i.e., duration of each behavior). Predictor variables were the different phases of the experiment. The second analysis addressed foraging habitat; we wanted to see if foraging time varied in different environments throughout the experiment. The target variable was the foraging time on each environment. Predictor variables were the different phases of the experiment.

For the first and second analyses, we ran generalized linear models (GLM) as proportion GLM in which success was considered to be the time spent on one activity and failure was the time spent on other activities (both durations were given as an input for this GLM). We therefore used a binomial distribution and a logit link function.

To the third analysis, we explored the influence of the experiment on the number of urban foraging events. The target variable was the number of urban foraging events per day divided by the observation duration multiplied by 100 (to have bigger estimates) as a response variable. Predictor variables were the different phases of the experiment, the different zones, as well as their interaction. The fourth analysis looked at the duration of foraging events in urban settings. We investigated whether there was a link between

the duration of urban foraging events and the number of participants in urban foraging events, the zone, and the study period. The target variable was the duration of urban foraging events. Predictor variables were the different phases of the experiment, the zone, and the number of participants to foraging events. For the third and fourth analyses, we ran linear models (LM) and checked visually for residuals normality and homoscedasticity. The fifth analysis focused on the number of participants in urban foraging events. For this, we looked at the influence of the period on the number of participants in urban foraging events in zone D, zone B, and in the unchanged zones (A and D). The target variable was the number of participants in urban foraging events. Predictor variables were the zones (respectively in zone D, zone B and in the unchanged zones (A and C)), the period, and their interaction. Because it was count data, we did a generalized linear model (GLM) with a Poisson distribution and a log link. However, because residuals showed overdispersion, we then switch to a GLM with negative binomial distribution.

In all analyses, we checked for collinearity: Explanatory variables show no significant collinearity (variance inflation factor (VIF) lower than 3). For each model, we used an information-theoretic approach to select the best model testing different combinations (Burnham and Anderson 2002). We used the second-order Akaike information criterion (AIC) to determine the level of support for each model, making it possible to carry out the model selection. We used the function dredge of the *MuMIn* package (Bartoń 2020). By convention, any model that falls within two AICc units of the lowest value is considered to fit the data equally well (Burnham and Anderson 2002). We thus verified that the best model was the one with the lowest AICc and that, ranking models according to AICc, the next model differed from the best by at least two AICc units. When relevant, we performed post hoc analyses on best models. We used the emmeans function from the package *emmeans* (Lenth 2020).

In addition, to deepen the analysis, three relating to the number of urban foraging events, we wanted to know if the number of urban foraging events in each zone differed in the four periods of the experiment. As the variables were discontinuous, a chi-square test was performed.

Finally, the last analysis focused on the initiators of urban foraging events. First, we wanted to know if the number of adult males, adult females, subadults, and juveniles initiating the urban foraging events varied during the experiment. Then, in a second time, we wanted to know if the number of baboons of each category (MA, FA, SA, J) initiating the urban foraging events changed depending on whether the zone has or does not have waste. A chi-square test was performed.

Results

Use of space

The troop of baboons changed the way it used the study area throughout the experiment. Indeed, the troop explored the south of its territory less during P2 and P3 than during P1 and P4 (Fig. 2). Changes were also observed for the use of sleeping sites, with the troop gradually abandoning southern sites during the food supply reduction experiment (Table 1).

Activity budget

Behavior

The behavior of the baboon troop varied across the different phases of the experiment (GLM, interaction: deviance = 1702.7, *df*: 12, $p < 0.01$; Fig. 3).

For the *exploration* behavior, post hoc tests showed significant differences between all pairwise comparisons. *Exploration* lasted significantly less time in P1 than in all other periods (P1 vs. P2: estimate = -0.143 , *se* = 0.051 , z value = -2.78 , $p = 0.028$; P1 vs. P3: estimate = -0.457 , *se* = 0.048 , z value = -9.44 , $p < 0.001$; P1 vs. P4: estimate = -0.662 , *se* = 0.048 , z value = -14.0 , $p < 0.001$), lasted significantly less time in P2 than in two other periods (P2 vs. P3: estimate = -0.314 , *se* = 0.048 , z value = -6.56 , $p < 0.001$; P2 vs. P4: estimate = -0.519 , *se* = 0.047 , z value = -11.1 , $p < 0.001$), and the duration of exploration was shorter in P3 than in P4 (P3 vs. P4: estimate = -0.205 , *se* = 0.044 , z value = -4.68 , $p < 0.001$).

For the foraging behavior, post hoc tests showed significant differences between all pairwise comparisons

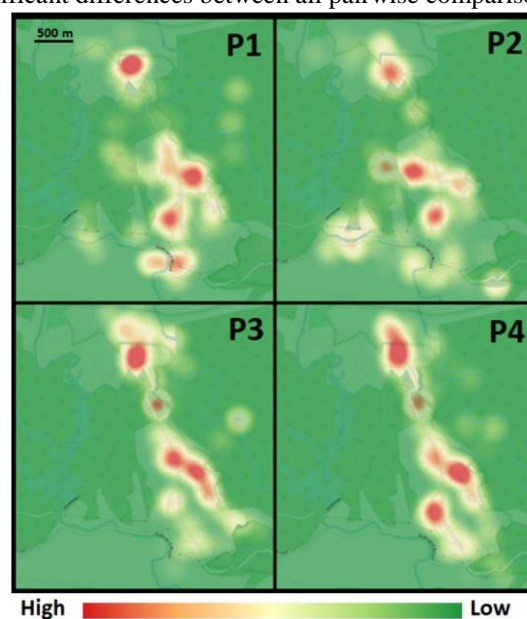


Table 1 Number of nights spent by Madiba's troop at each sleeping site for each period of the experiment

	Sleeping site	Sa	Sb	Sc	Sd	Se
<i>P</i> <i>I</i>	P1	4	0	6	1	4
	P2	3	5	2	3	2
	P3	6	6	2	0	1
	P4	6	4	5	0	0

n

o reduction of food supply period, *P2* food supply reduction period in zone D, *P3* food supply reduction period in zone D and B, and *P4* no reduction of food supply period

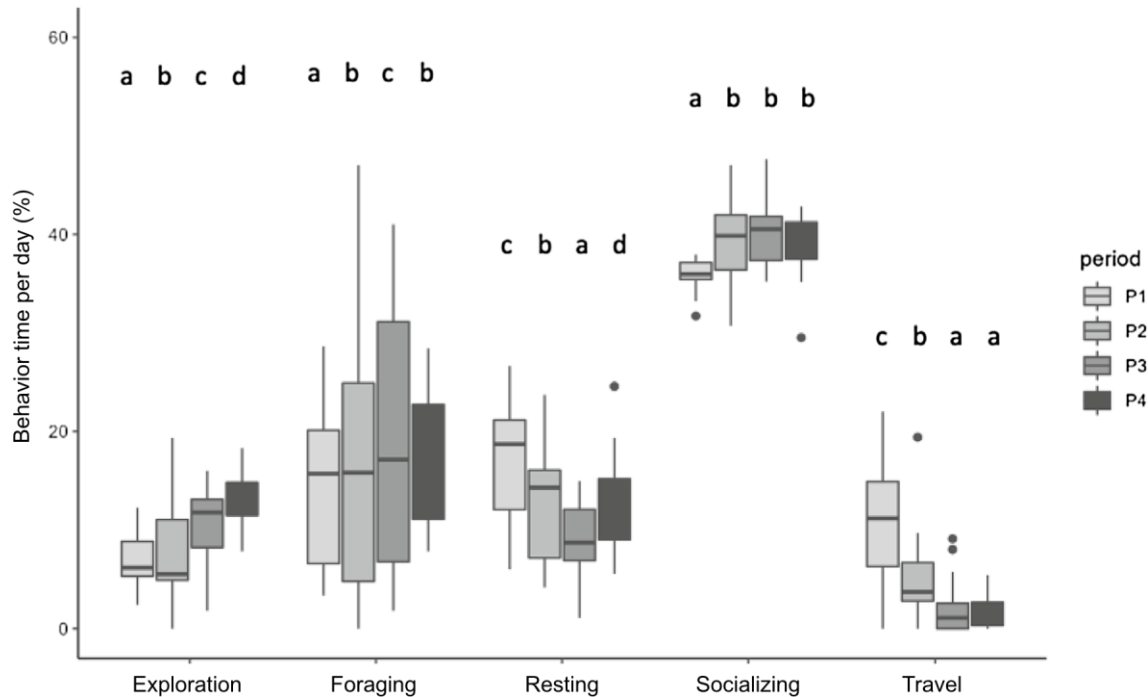


Fig. 2 Exploitation of the environment of the troop during the experiment. P1: no reduction of food supply period, P2: food supply reduction period in zone D, P3: food supply reduction period in zone D and B, and P4: no reduction of food supply period. The color gradient corresponds to the intensity of exploitation of the environment by the troop: the redder it is, the more the zone was frequented

except between P2 and P4: foraging lasted significantly less time in P1 than in all other periods (P1 vs. P2: estimate = -0.174 , se = 0.026 , z value = -6.69 , $p < 0.001$; P1 vs. P3: estimate = -0.278 , se = 0.026 , z value = -10.8 , $p < 0.001$; P1 vs. P4: estimate = -0.129 , se = 0.027 , z value = -4.83 , $p < 0.001$), it lasted significantly less time in P2 than in P3 but there was no difference between P2 and P4 (P2 vs. P3: estimate = -0.104 , se = 0.026 , z value = -4.07 , $p < 0.001$; P2 vs. P4: estimate = 0.046 , se = 0.027 , z value = 1.73 , $p = 0.310$), and lasted significantly more time in P3 than in P4 (P3 vs. P4: estimate = 0.149 , se = 0.026 , z value = 5.72 , $p < 0.001$).

For the resting behavior, post hoc tests showed significant differences between all pairwise comparisons except between P2 and P4. Resting lasted significantly more time in P1 than in all other periods (P1 vs. P2: estimate = 0.308 , se

= 0.038 , z value = -6.69 , $p < 0.001$; P1 vs. P3: estimate = 0.670 , se = 0.042 , z value = 16.0 , $p < 0.001$; P1 vs. P4: estimate = 0.329 , se = 0.039 , z value = 8.37 , $p < 0.001$), and lasted significantly more time in P2 than in P3 (P2 vs. P3: estimate = 0.361 , se = 0.045 , z value = 8.12 , $p < 0.001$) but there was no difference between P2 and P4 (estimate = 0.021 , se = 0.042 , z value = 0.487 , $p = 0.962$). Finally, resting lasted significantly less time in P3 than in P4 (P3 vs. P4: estimate = -0.341 , se = 0.045 , z value = -7.53 , $p < 0.001$).

Fig. 3 Duration of behavior per day (%) depending on the periods of the experiment. P1: no reduction of food supply period, P2: food supply reduction period in zone D, P3: food supply reduction period in zone D and B, and P4: no reduction of food supply period. Different

letters indicate statistical significance ($p < 0.05$). The same letters mean that no statistically significant difference was found between the

For the socializing behavior, pairwise tests showed significant differences between P1 and the other periods with less time devoted to socializing in P1 than in other periods (P1 vs. P2: estimate = -0.130 , se = 0.028 , t value = -4.64 , $p = 1$; P1 vs. P3: estimate = -0.174 , se = 0.028 , t value = -6.20 , $p < 0.001$; P1 vs. P4: estimate = -0.145 , se = 0.029 , t value = -5.08 , $p < 0.001$) and no significant differences between the other pairwise comparisons (P2 vs. P3: estimate = -0.044 , se = 0.028 , t value = -1.54 , $p = 0.414$; P2 vs. P4: estimate = -0.014 , se = 0.029 , t value = -0.501 , $p = 0.959$; P3 vs. P4: estimate = 0.029 , se = 0.029 , t value = 1.01 , $p = 0.741$).

For travel behavior, post hoc tests showed significant differences between all pairwise comparisons except between P3 and P4. Baboons traveled significantly more time in P1 than in all other periods (P1 vs. P2: estimate = 0.697 , se = 0.053 , z value = -13.1 , $p < 0.001$; P1 vs. P3: estimate = 1.64 , se = 0.074 , z value = 22.1 , $p < 0.001$; P1 vs. P4: estimate = 1.85 , se = 0.083 , z value = 22.4 , $p < 0.001$).

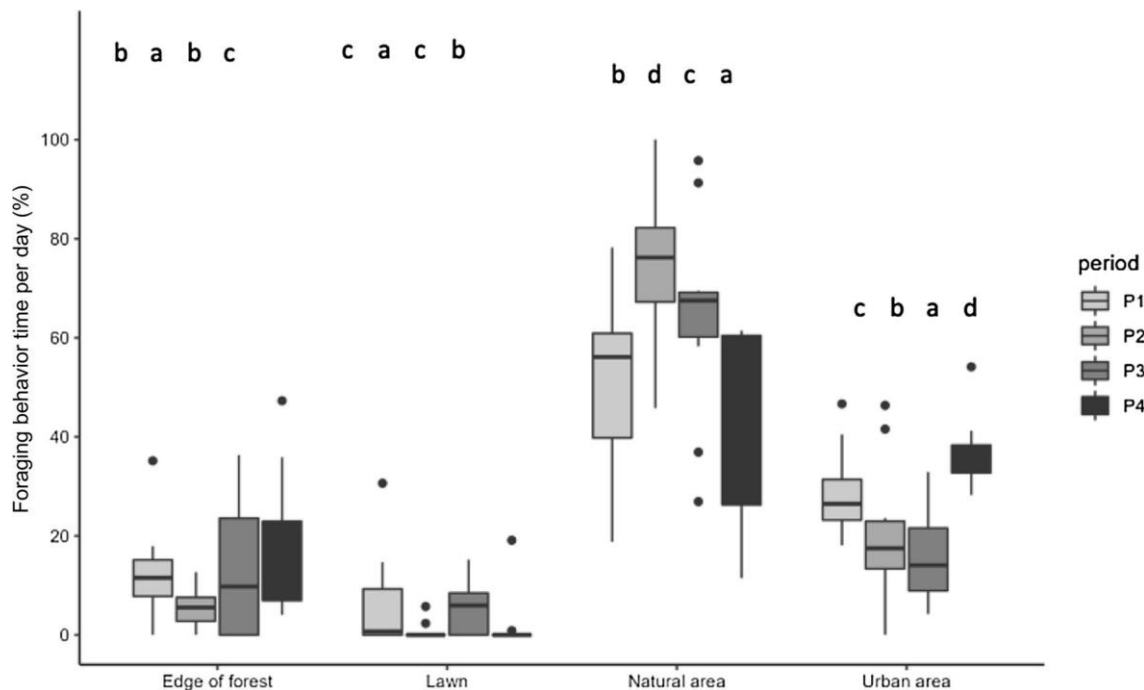
periods. Different letters mean that a statistically significant difference was found between the periods

0.001), and more time in P2 than in the two other periods (P2 vs. P3: estimate = 0.943 , se = 0.080 , z value = 11.8 , $p < 0.001$; P2 vs. P4: estimate = 1.15 , se = 0.088 , z value = 13.1 , $p < 0.001$). No difference in time spent traveling was observed between P3 and P4 (estimate = 0.021 , se = 0.102 , z value = 2.07 , $p = 0.163$).

Foraging habitats

The foraging time budget of the baboon troop varied between habitats over the course of the experiment (GLM, interaction: Deviance = 1173 , df : 144), $p < 0.01$; Fig. 4).

Fig. 4 Foraging time per day (%) depending on the environment and the periods of the experiment. P1: no reduction of food supply period, P2: food supply reduction period in zone D, P3: food supply reduction period in zone D and B, and P4: no reduction of food supply period. Different letters indicate statistical significance ($p < 0.05$). The same letters mean that no statistically significant difference was found between the periods. Different letters mean that a statistically significant difference was found between the periods



At the edge of the forest, post hoc tests showed significant differences between all pairwise comparisons except between P1 and P3 (P1 vs. P3: estimate = -0.052 , se = 0.085 , z value = -0.607 , $p = 0.930$). Time spent foraging at the edge of the forest was significantly longer in P1 than in P2 (P1 vs. P2: estimate = 0.949 , se = 0.108 , z value = 8.79 , $p < 0.001$), no difference was found between P1 and P3 (P1 vs. P3: estimate = -0.052 , se = 0.085 , z

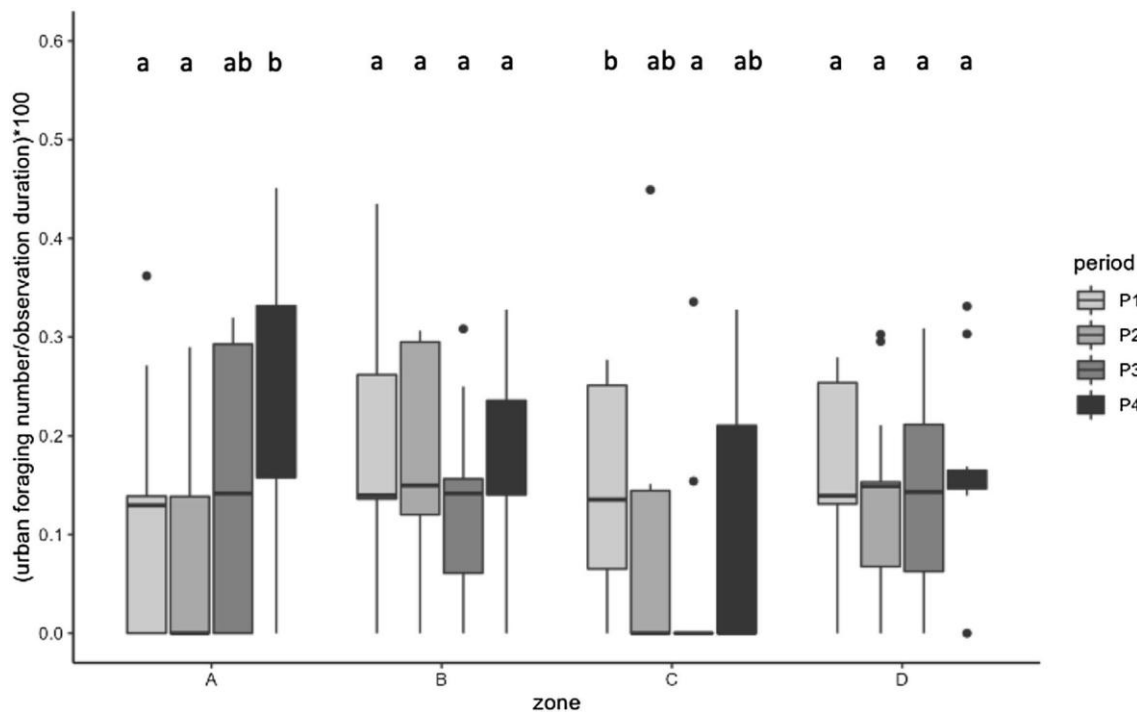
value = -0.607 , $p = 0.930$) and baboons spent significantly more time at the edge of the forest in P4 than in P1 (P1 vs. P4: estimate = -0.350 , se = 0.085 , z value = -4.12 , $p < 0.001$). Time spent foraging at the edge of the forest was significantly shorter in P2 than in P3 and P4 (P2 vs. P3: estimate = -1.00 , se = 0.105 , z value = -9.54 , $p < 0.001$; P2 vs. P4: estimate = -1.30 , se = 0.105 , z value = -12.4 ,

$p < 0.001$), and shorter in P3 than in P4 (P3 vs. P4: estimate = -0.298 , $se = 0.081$, z value = -3.69 , $p = 0.001$).

At the lawn, pairwise post hoc tests showed significant differences between all pairwise comparisons except between P1 and P3. Time spent at the lawn was significantly longer in P1 than in P2 and P4 and no difference was found between P1 and P3 (P1 vs. P2: estimate = 2.30 , $se = 0.256$, z value = 8.99 , $p < 0.001$; P1 vs. P3: estimate = 0.208 , $se = 0.123$, z value = 1.68 , $p = 0.330$; P1 vs. P4: estimate = 1.35 , $se = 0.186$, z value = 7.27 , $p < 0.001$). Baboons spent significantly less time at the lawn in P2 than in P3 and P4 (P2 vs. P3: estimate = -2.09 , $se = 0.257$, z value = -8.16 , $p < 0.001$; P2 vs. P4: estimate

(P3 vs. P4: estimate = 0.810 , $se = 0.059$, z value = 13.6 , $p < 0.001$).

Finally, at the urban area, pairwise post hoc tests showed significant differences between all pairwise comparisons. Baboons spent significantly more time foraging in urban area in P1 than in P2 and P3 and less time in P1 than in P4 (P1 vs. P2: estimate = 0.514 , $se = 0.068$, z value = 7.61 , $p < 0.001$; P1 vs. P3: estimate = 0.753 , $se = 0.070$, z value = 10.8 , $p < 0.001$; P1 vs. P4: estimate = -0.300 , $se = 0.064$, z value = -4.60 , $p < 0.001$). They spent significantly more time foraging in urban area in P2 than in P3 but less time in P2 than in P4 (P2 vs. P3: estimate = 0.238 , $se = 0.072$, z value = 3.29 , $p < 0.001$; P2 vs. P4: estimate = -0.810 , $se =$



= -0.946 , $se = 0.292$, z value = -3.24 , $p = 0.007$). Time spent foraging at the lawn was significantly longer in P3 than in P4 (P3 vs. P4: estimate = 1.15 , $se = 0.187$, z value = 6.13 , $p < 0.001$).

At the natural area, pairwise post hoc tests showed significant differences between all pairwise comparisons. Baboons spent significantly less time foraging in the natural area in P1 than in P2 and P3 but more time in P1 than in P4 (P1 vs. P2: estimate = -0.986 , $se = 0.062$, z value = -16.0 , $p < 0.001$; P1 vs. P3: estimate = -0.559 , $se = 0.059$, z value = -9.54 , $p < 0.001$; P1 vs. P4: estimate = 0.251 , $se = 0.060$, z value = 4.17 , $p < 0.001$). They spent significantly more time foraging in natural area in P2 than in P3 and P4 (P2 vs. P3: estimate = 0.427 , $se = 0.061$, z value = 7.01 , $p < 0.001$; P2 vs. P4: estimate = 1.24 , $se = 0.062$, z value = 19.9 , $p < 0.001$) and more in P3 than in P4

(P3 vs. P4: estimate = -1.05 , $se = 0.069$, z value = -15.1 , $p < 0.001$).

Urban foraging

Number of urban foraging events

A total of 228 urban foraging events were recorded in 60 days across the four zones. However, the events were not evenly distributed throughout the experiment (LM: $F = 3.39$, $df: 15; 224$, $p < 0.001$).

When comparing the number of events for each zone according to the different phases (Fig. 5), for zone A (unchanged area), pairwise post hoc tests showed significant differences between some periods (P1 vs. P4: estimate = -0.144 , $se = 0.041$, t value = -3.53 , $p = 0.003$; P2

vs. P4: estimate = -0.176 , se = 0.041 , t value = -4.30 , $p < 0.001$) but not for others (P1 vs. P2: estimate = 0.032 , se = 0.041 , t value = 0.776 , $p = 0.866$; P1 vs. P3: estimate = -0.043 , se = 0.041 , t value = -1.05 , $p = 0.719$; P2 vs. P3: estimate = -0.075 , se = 0.041 , t value = -1.83 , $p = 0.263$; P3 vs. P4: estimate = -0.101 , se = 0.041 , t value = -2.48 , $p = 0.067$).

For zone B (waste-free area in P3), pairwise post hoc tests showed no significant differences between periods (P1 vs. P2: estimate = 0.012 , se = 0.041 , t value = 0.288 , $p = 0.992$; P1 vs. P3: estimate = 0.063 , se = 0.041 , t value = 1.53 , $p = 0.421$; P1 vs. P4: estimate = 0.013 , se = 0.041 , t value = -0.308 , $p = 0.990$; P2 vs. P3: estimate = 0.051 , se =

0.041 , t value = 1.24 , $p = 0.601$; P2 vs. P4: estimate = 0.001 , se = 0.041 , t value = 0.020 , $p = 1.00$; P3 vs. P4: estimate = -0.050 , se = 0.041 , t value = -1.22 , $p = 0.614$).

For zone C (unchanged area), except for a significant difference between P1 and P3 (P1 vs. P3: estimate = 0.116 , se = 0.041 , t value = 2.84 , $p = 0.025$), the pairwise post hoc tests showed no significant differences between periods (P1 vs. P2: estimate = 0.080 , se = 0.041 , t value = 1.95 , $p = 0.211$; P1 vs. P4: estimate = 0.047 , se = 0.041 , t value = 1.16 , $p = 0.654$; P2 vs. P3: estimate = 0.037 , se = 0.041 , t value = 0.893 , $p = 0.809$; P2 vs. P4: estimate = -0.032 , se = 0.041 , t value = -0.790 , $p = 0.859$; P3 vs. P4: estimate = -0.070 , se = 0.041 , t value = -1.68 , $p = 0.335$).

Number of participants

The best model included only the variable period. However, pairwise post hoc tests only showed a tendency between P3 and P4 (P3 vs. P4: estimate = -0.475 , se = 0.192 , z value = -2.47 , $p = 0.065$) but not with the others (P1 vs. P2: estimate = 0.001 , se = 0.193 , z value = 0.006 , $p = 1.00$; P1 vs. P3: estimate = 0.142 , se = 0.193 , z value = 0.735 , $p = 0.883$; P1 vs. P4: estimate = -0.333 , se = 0.192 , z value = -1.73 , $p = 0.307$; P2 vs. P3: estimate = 0.141 , se = 0.193 , z value = 0.729 , $p = 0.886$; P2 vs. P4: estimate = -0.334 , se = 0.192 , z value = -1.74 , $p = 0.304$) (Fig. 6).

Fig. 5 Number of urban foraging divided by the duration of observation and multiplied by 100 afterwards over zones and periods. B and D were the waste-free zones, A and C were the unchanged zones. P1: no reduction of food supply period, P2: food supply reduction period in zone D, P3: food supply reduction period in zone D and B, and P4: no reduction of food supply period (within each zone, *different letters* indicate statistical significance ($p < 0.05$)). The same letters mean that no statistically significant difference was found between the periods. *Different letters* mean that a statistically significant difference was found between the periods

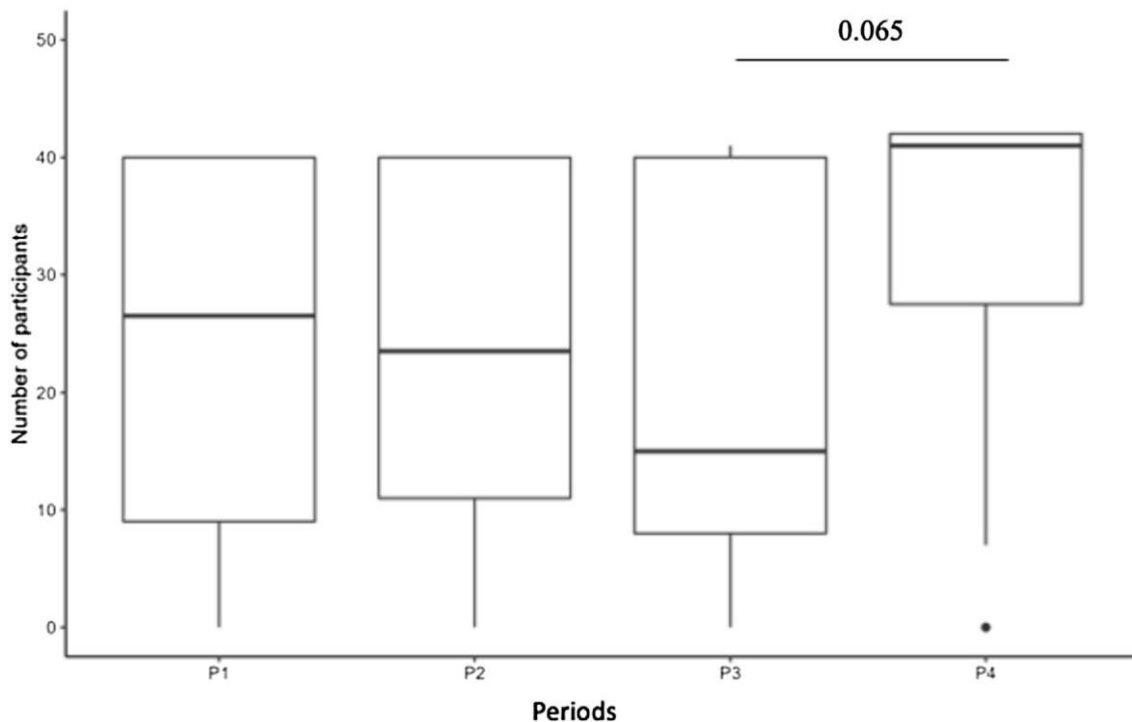
For zone D (waste-free area in P2 and P3), pairwise post hoc tests showed no significant differences between periods (P1 vs. P2: estimate = 0.043 , se = 0.041 , t value = 1.05 , $p = 0.720$; P1 vs. P3: estimate = 0.030 , se = 0.041 , t value = 0.742 , $p = 0.880$; P1 vs. P4: estimate = 0.009 , se = 0.041 , t value = -0.225 , $p = 0.996$; P2 vs. P3: estimate = -0.013 , se = 0.041 , t value = -0.309 , $p = 0.990$; P2 vs. P4: estimate = -0.034 , se = 0.041 , t value = -0.826 , $p = 0.842$; P3 vs. P4: estimate = -0.021 , se = 0.041 , t value = -0.517 , $p = 0.955$).

Duration of urban foraging events

The best model did not include the period variable. Results from linear model showed a significant effect of the number of participants: the higher the number of participants, the longer of duration of raid (estimate = 0.769 , se = 0.110 , t -ratio = 6.98 , $p < 0.001$). Pairwise post hoc tests significant differences between some zones (A vs. B: estimate = 13.7 , se = 4.43 , t -ratio = 3.09 , $p = 0.012$; B vs. D: estimate = -16.4 , se = 4.48 , t -ratio = -3.67 , $p = 0.002$) but not for the others (A vs. C: estimate = 9.66 , se = 5.19 , t -ratio = 1.86 , $p = 0.248$; A vs. D: estimate = -2.76 , se = 4.59 , t -ratio = -0.601 , $p = 0.932$; B vs. C: estimate = -4.02 , se = 5.08 , t -ratio = -0.792 , $p = 0.858$; C vs. D: estimate = -12.4 , se = 5.23 , t -ratio = -2.37 , $p = 0.085$). Zone B was frequented for less time than zones A and D.

Initiator

During the experiment, adult males initiated the majority of urban foraging events (83,0%), while adult females and the subadults initiated only 10.3 and 6.7%, respectively. No difference was found in the distribution of the urban foraging event initiations between the different phases of the experiment (chi-square test: $\chi^2 = 8.00$, $df: 6$, $p = 0.24$) and the type of zones (with or without waste) (chi-square test: $\chi^2 = 2.4$, $df: 2$, $p = 0.3$). With regards female initiations, we noted that only females without infants initiated urban foraging events. Juveniles never initiated an event.



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Fig. 6 Number of participants per urban foraging event as a function of the period. P1: no reduction of food supply period, P2: food supply reduction period in zone D, P3: food supply reduction period in zone D and B, and P4: no reduction of food supply period

Discussion

The aim of this study was to observe and understand the strategies displayed by a baboon troop in response to the management of anthropogenic resources in a periurban environment. To this end, we designed an experiment in which all waste in a first phase was continuously removed from a specific zone of a peri-urban area where the baboons regularly foraged and from two areas in a second phase. Our results showed significant effects of this experimental manipulation on the troop behavior and highlight that baboons changed their foraging strategies to deal with this altered environment.

Consequences of food resource management on the baboon activity budget and use of space

The activity budget of the baboon troop varied during the different phases of anthropogenic food supply reduction (cf. Fig. 3). The adjustment of foraging time also differed according to the extent of anthropogenic food deprivation (cf. Fig. 4). When anthropogenic food was removed from the main site where the troop foraged (zone D), the baboons increased their foraging in their natural environment and decreased the time spent foraging in urban area. Foraging on natural food takes more time (Warren et al. 2011) since natural food is less rich in energy and requires more time to collect and/or process than anthropogenic food (ForthmanQuick and Demment 1988). The location of natural food is also more widely dispersed and less predictable than that of anthropogenic food, which is concentrated in bins, refrigerators, or cupboards. Despite the outstanding cognitive abilities of baboons (i.e., cognitive map), finding trees with mature fruits is time-consuming (Warren et al. 2011). This increase in foraging time during the first anthropogenic food supply reduction phase was likely due to the decreased availability of anthropogenic food. This caused a significant depletion of resources for the baboons. Consequently, they were forced to allocate more time and energy to foraging in natural environments. Surprisingly, from P2 to P4, baboons decreased the time spent foraging in the natural environment. This result may be due to the depletion of natural food by the baboons themselves during P2 since they mainly foraged on natural food during this phase.

When the waste-free zone was extended in the second experimental phase (P3), baboons decreased even more their foraging time in urban area, suggesting that they were discouraged by the lack of food. Interestingly, in this period, the troop changed its strategy and stayed closer to the peri-urban environment than during P2. From this location, the baboons were able to monitor the peri-urban

environment, and thus increased their chances to find anthropogenic food (Dunbar and Nathan 1972; Else 1991) while concomitantly foraging in the forest. This is reminiscent of the “sit and wait” strategy previously reported in other baboon troops (Strum 1994; van Doorn et al. 2010, Fehlmann et al. 2017b). For instance, we observed several occasions when baboons came out of the forest immediately after a human had put waste in a bin.

These changes in foraging strategy had implications for the troop activity budget (cf. Fig. 3). During the course of our experiment, the time devoted to foraging increased because of longer foraging bouts on natural resources but also because the troop explored the peri-urban environment for longer periods of time due to the absence of waste at several locations. It is possible that the troop had to invest more time in obtaining its daily food quota and logically, resting time decreased.

Time allocated to socializing (comprising affiliative and agonistic interactions) was smaller in P1 compared to all other periods. These differences in socializing may have been due to higher frequency of agonistic interactions due to increased contest competition over food. Indeed, the scarcity of food amplified intra-group competition to access anthropogenic food, as illustrated by an increase in conflicts between primarily male adults (Mazué, personal observation) and a gradual decrease in troop cohesion. In addition, the increased splintering of the troop due to increased scramble competition may have then led to increased male-male competition over more widely dispersed females (Barton et al. 1996). However, more quantitative, and detailed data are needed to confirm these results. Interestingly, the troop traveled more in P1 than in all other periods and more in P2 than in P3 and P4, suggesting that in response to the scarcity of food, the troop minimized its movements across the environment perhaps to save energy (Fehlmann et al. 2017a, b). This result is consistent with the troop preference for the forest edge, which limits the distance to be traveled for finding food (because it is close to natural and urban areas). Finally, a rebound effect is observed in P4 (compared to P1) with an increased use of the urban area and an increase in exploration and foraging. This effect suggests the strong dependence of the troop on anthropogenic waste.

Urban foraging and changes in the frequented area

The number of urban foraging events was unchanged in the waste-free areas (zones B and D) during the study period (cf. Fig. 5). This result suggests that, when foraging, baboons insisted on these two preferred areas. Furthermore, it is important to remember that only part of the food supply was removed from the peri-urban area. Even if we removed waste from the bins, the baboons could still gain

access to houses and the anthropogenic food inside them, and there were still areas with waste to exploit. It is therefore not surprising that urban foraging continued throughout the experiment. Moreover, these zones (especially D) usually contained the highest amount of anthropogenic food and was generally the first site visited by the baboons during the day. Nevertheless, a decrease was observed in the number of urban foraging events in zone C (close to B and D) during the second food supply reduction step (P3). The food uncertainty in the middle of the campus in P3 may have led the troop to gradually abandon the southern part of the campus in favor of the northern area to exploit the other zones and thus optimize their foraging effort (cf. Fig. 2). In terms of natural food, there is less African forest in the southern zone, and it is less dense than in the north, the rest being grassland. Another reason might have pushed the baboons to the north. Just below the lowest site (in the south) is a busy road, with lots of traffic that does not always slow down at the sight of the monkeys, and on the other side of the road is a farm that shoots the monkeys with guns and bows. These findings are supported by the fact that the northern sleeping sites were more frequently used at night during this phase than during the other phases, while the two southern sleeping sites were completely abandoned. Other studies have shown that urban-foraging baboons minimize the distance between their sleeping sites and foraging spots (Hoffman and O’Riain 2012; Fehlmann et al. 2017a, b). Our results suggest that during the phase of extreme food supply reduction, baboons seek to save energy by sleeping close to the richest foraging zones. This also shows that the zones between urban areas and natural areas are strategic areas for baboons because they maximize the diversity of foraging options. This may explain why the troop has chosen to focus on a n area which concentrated both anthropogenic and natural food in great quantities as illustrated by the highest use of zone A in P4 compared to other periods and zones.

During the experiment, despite waste depletion, the urban foraging events duration did not change in zone D. We can assume that baboons insisted on their preferred foraging area and that the time usually allocated to foraging and eating food from bins has been converted into foraging time in buildings. However, our method did not allow the estimation of time spent foraging in bins and/ or houses. In comparison, the duration of urban foraging events in zones B (waste-free) and C (unchanged) has decreased, suggesting that the time spent insisting on zone D may have limited the time spent in these nearby zones. In addition, the experiment had no effect on the duration of urban foraging events in zone A (unchanged).

Participants in urban foraging events and individual strategies

The number of participants in urban foraging events did not vary during the experiment but a slight rebound effect was observed in P4 with a higher number of participants than in P3 (cf. Fig. 6). If we look more specifically at zone D, there were less participants in P3 compared to P1 but more individuals participating in P4. Overall, these results illustrate the high dependence of baboons on anthropogenic waste as they performed more urban foraging when conditions returned to normal than before the experiment.

The males, and especially the dominant ones, were usually the initiators of actions when baboons arrived at an urban foraging site. They were followed by subadult individuals (males or females) and adult females without infants. It has been reported that females with infants and their juveniles only came when the first participants had finished exploring the bins (Kaplan et al. 2011). There are therefore differences in strategies within the troop depending on the age and sex of the individuals.

Perspectives

Our experience of reducing the food supply has shown how dependent baboons are on human food and how crucial waste management is to improving coexistence between humans and baboons. As baboons chose to ‘abandon’ the southern part of the campus during this experiment, presumably due to a generalization of the absence of waste (from B & D to C), the removal of food from the different zones could be tested randomly to reduce the predictability of the presence of anthropogenic food. Such an approach will definitely increase the cost of foraging in the urban area for baboons and help pushing them back to the forest (cf. Kaplan et al. 2011). However, to be truly effective, the food supply would have to be eliminated from the entire urban area (through better waste management, baboonproof bins and the systematic closing of doors and windows). Indeed, the passive management of human–baboon conflicts in peri-urban areas would only be guaranteed by completely removing access to anthropogenic resources.

Supplementary Information The online version contains supplementary material available at <https://doi.org/10.1007/s10329-022-01032-x>.

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Data availability The Daily data (environment + behaviour) and the data of urban foraging events that support the findings of this study are available in Zenodo digital repository with the identifier(s) data DOI(e) e.g. <https://doi.org/10.5281/zenodo.7358546>.

Declarations

Conflict of interest The authors have no relevant financial or non-financial interests to disclose.

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