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Influence of Visitors on the Time Budget, Ranging and Strata Use of Lowe's Monkey (*Cercopithecus lowei*) at Boabeng-Fiema Monkey Sanctuary, Ghana

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Wildlife tourism could be a conservation tool; however, it may disrupt the natural behaviors of wild animals. We examined how wildlife tourism affects Lowe's monkeys (*Cercopithecus lowei*) at the Boabeng-Fiema Monkey Sanctuary, central Ghana. We examined and compared the time budget, aggression patterns, home range size and strata use of two *C. lowei* groups—one with a high level of provisioning by visitors/tour guides (HP group) versus one with a low level of provisioning by visitors/tour guides (LP group). We found evidence that the HP group fed less and rested more than the LP group. The HP group significantly increased the time spent feeding and decreased their time resting, but no significant differences were recorded for moving or socializing either in the presence of small or big groups of visitors (*i.e.*, 1–10 visitors or > 10 visitors). In the presence of one to ten visitors, the HP group monkeys increased the use of ground by 22.10% and decreased the use of medium and high tree strata by 15.43% and 11.6%, respectively. Agonistic behaviors (*i.e.*, threat, chase, and attack) were three times higher in the HP group (*e.g.*, open-jawed gaze gesture or head-bobbing). In the presence of visitors, aggression in the HP group increased from 12.81% to 30.18%. The home range size of the *C. lowei* HP group was smaller (4.68 ha) compared to the LP group (14.25 ha) (*i.e.*, 50.56% difference). The LP group spent significantly less time socializing and more time moving. They fed more on fruits and insects. On average, the daily travel of LP group was 0.58 km more than the HP group (*i.e.*, 22.80% difference), and the former group also spent significantly more time in the mid strata of the canopy. Our results showed that continued provisioning of the monkeys with human foods is detrimental to their natural behavior of the monkeys and could have negative long-term effects on the conservation efforts for the species.

Key words: Activity Pattern, Aggression, *Cercopithecus lowei*, Home Range, Strata, Wildlife Tourism.

BACKGROUND

Wildlife tourism—where leisure is mixed with education, nature conservation, and cultural awareness—is becoming increasingly popular in wild areas (Reynolds and Braithwaite 2001). Feeding wild animals is sometimes part of wildlife tourism and is often a popular tourist activity that may have a positive or negative impact on wild animals (Maréchal et al. 2016a). Two positive impacts could be income generation from the

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fees to support the site or local people (Orams 2002; Watermeyer et al. 2011), which improve local attitudes towards conservation, and the management of human-primate interactions (Unwin and Smith 2010). Some of the negative consequences documented include environmental pollution, ecosystem degradation, short- or long-term changes in animal populations, and changes in community lifestyle in the surrounding area (Reynolds and Braithwaite 2001; Green and Giese 2004). Primate ranging patterns are influenced by several ecological and behavioral factors; for example, seasons, food availability, food distribution and quality, availability of water, group size, and sleeping and resting sites (Fashing 2001). Wildlife tourism and tourist provisioning may disrupt the natural behaviors of wildlife, reduce their health (Stockin et al. 2008; Maréchal et al. 2016b), and affect their distribution (Shannon et al. 2017). For example, howler monkeys at a Belizean archaeological site increased the use of ground strata when visitors were present, increasing predation and disease transmission risks (Grossberg et al. 2003); pygmy marmosets in Ecuadorian Amazonia reduced social play and vocalizations, and increased use of lower strata to avoid contact with humans (de la Torre et al. 2000); and rhesus macaques spent more time on human-modified areas than forest areas when provisioning was available on the Buxa Tiger Reserve, India (Sengupta and Radhakrishna 2018).

Tourist feeding of wildlife is an important issue that needs attention, both at Boabeng-Fiema Monkey Sanctuary (BFMS) and elsewhere (Orams 2002). Deliberate feeding of the monkeys at the BFMS raises particular concerns because it may detrimentally affect the natural behavior of the monkeys; feeding also poses health risks (*i.e.*, monkey bites, disease transfer) to the visitors and the monkeys alike. It has become a habit for tour guides in BFMS to feed Lowes monkeys during tours in an effort to allow visitors to see and interact closely with the monkeys. The provision of supplemental food to wildlife can affect the monkeys natural feeding and foraging behavior (Shannon et al. 2017). It affects the composition of the diet and alters the amount of food and the nutrients ingested (Wrangham 1974; Asquith 1989; McKinney 2011; Kreigenhofer 2017). It also has the potential to change the home range location and size (Boutin 1990; Sengupta and Radhakrishna 2018), affecting the ecosystem as well through changes in the eco-ethology of the animals (Sengupta et al. 2015). There is currently a lack of information on *C. lowei* in relation to the effects of wildlife tourism on this species in their natural environment and even for other species, as such research is typically conducted in zoos (Chamove et al. 1988; Cook and Hosey 1995; Mallapur et al. 2005; Stevens et al. 2013).

The BFMS in central Ghana harbours two primates of conservation concern under the IUCN Red List of threatened species—the *Cercopithecus lowei* (Lowe's monkey, vulnerable) and *Colobus vellerosus* (White-thighed colobus monkey, critically endangered) (Wiafe et al. 2019; Matsuda et al. 2020)—along with a nocturnal primate (Galago senegalensis) (Bearder, unpublished report). Killing Lowe's monkeys is taboo and traditionally illegal in the BFMS (Fargey 1991). There are no interspecific competitions over resources in the foraging range of the monkeys because *C. vellerosus* naturally feed on leaves (Onderdonk and Chapman 2000; Saj and Sicotte 2007), *C. lowei* diet consists more fruits (Porter 2005), whereas *Galago senegalensis* is nocturnal and feeds predominantly on plant exudates and invertebrate (Nash et al. 2013). The monkey population has increased over the years (Kankam et al. 2010), since a hunting ban was enacted in the mid-1970s (Saj et al. 2005). Fargey (1991) recorded 216 Lowe's monkeys in 1990, and Kankam (1997) recorded 342 individuals in 1997 and more than 400 individuals in 2007 in BFMS and surrounding communities (Kankam B. O. unpublished data). The *C. lowei*'s diet is mainly composed of fruit, although it also consumes different proportions of invertebrates, vertebrates, flowers, leaves, seeds and gum (Enstam and Isbell 2007). Previous studies in the BFMS have indicated that some *C. lowei* groups may spend approximately 50% of their time feeding time eating garbage and cultivated foods (Fargey 1991; Porter 2005). The monkeys are generally found at the low and medium stratum (< 10 m) (Porter 2005). The group size ranges from 10 to over 27 individuals (Fargey 1991), and uses an area of 14.5 ha at the BFMS (Porter 2005).

The monkey sanctuary, which doubles as a wildlife tourism centre, attracts visitors from Ghana and other parts of the world. Visitors' numbers to BFMS have continued to increase, since the wildlife tourism project began, from about 150 visitors in 1990 (Fargey 1991) to more than 14,000 visitors in 2007 (Kankam et al. 2010). There has been a consistent increase in the number of visitors to BMFS to more than 18,000 in recent years (Badiella-Giménez 2015). Visitors to BFMS have the opportunity to enjoy close-up views of free-ranging primates, especially some of the Lowe's monkeys who sometimes move around the villages looking for human food (Fargey 1991; Briggs 2011).

This study examined how wildlife tourism affects the behavior of *C. lowei* monkeys in BFMS. Specifically, we compared the activity budgets and ranges of two groups of *C. lowei* (high-level provisioning group and low-level provisioning group). We documented and compared *C. lowei* agonistic

behaviors, home range size, and canopy use within and between these groups. We hypothesized that the feeding of the monkeys by visitors or tour guides negatively influence the natural behaviors of the monkeys (Doenier et al. 1997). Specifically, we expected that the HP group would spend more time feeding on enrichment food provided by visitors compared to the LP *C. lowei* group. Second, we hypothesized that the presence of visitors would increase aggression towards within-group conspecifics (Hsu et al. 2009), especially in a HP group due to the anticipation of a clumped, high-quality resource being available. Third, we hypothesized that a high level of provisioning *C. lowei* groups by visitors would reduce the home range size at BFMS. Finally, we hypothesized that the Lowe's monkey HP group would be more likely to alter their use of forest canopy strata and more frequently use lower and medium strata in response to high tourist numbers and relative to the LP group (de la Torre et al. 2000).

MATERIALS AND METHODS

Study area

The Boabeng-Fiema Monkey Sanctuary is a community protected forest situated within the transition zone of Ghana (7°42'N, 1°41'W). The BFMS is approximately 496 ha, but only the core forest (*i.e.*, about 190 ha) is protected from anthropogenic activities. The sanctuary is an isolated forest surrounded by villages associated with smaller forest fragments, ranging from 3.2 ha to 74.9 ha (Wong and Sicotte 2006; Kankam et al. 2010) (Fig. 1). The surrounding fragments—Senya (74.9 ha), Akrudwa kuma (34.2 ha), Bonte (33.5 ha), Bomini (31 ha), and Konkrompe (38.9 ha)—have four, seven, two, one and eight Lowe's monkey individuals, respectively, in their remnant forests. The others—Busunya (54.1 ha), Tankor (6.8 ha), Akrudwa pinyin (3.2 ha), and Kwaase (4.9 ha)—have

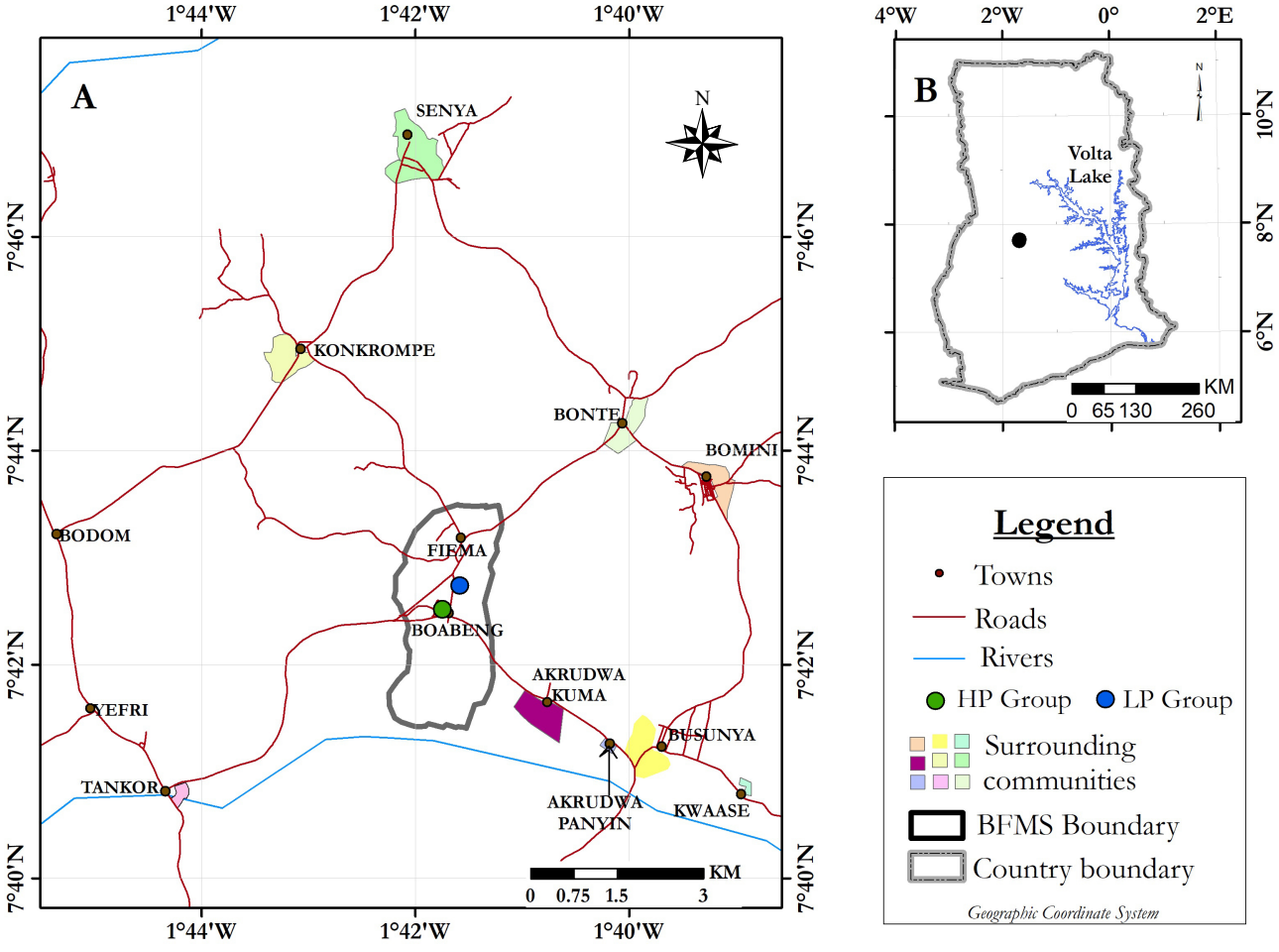

Fig. 1. Map of the Boabeng-Fiema Monkey Sanctuary (black contour line demarcates the core area of the sanctuary), eight surrounding communities (polygons in colors), and the location of the study groups (green dot: high-level provisioned group; blue dot: low-level provisioned group). Grey lines represent vehicular roads.

no Lowe's monkeys in their forests (Kankam B. O. unpublished data). A census conducted by Kankam in 2007 recorded 481 individuals in 36 groups in BFMS, and 22 individuals in five groups in the surrounding communities totalling 503 individuals in 41 groups (Kankam B. O. unpublished data). The sanctuary is also home to one nocturnal primate (*Galago senegalensis*), 375 species of butterflies (Larsen et al. 2009), and fruit bats. Medium to large mammals are rarely present due to hunting (Kankam et al. 2010). The vegetation is characterized by forest and savannah woodland vegetation with patches of undisturbed forest (Swaine et al. 1976; Hall and Swaine 1981; Kankam et al. 2010; Kankam and Sicotte 2013). There is also regenerating farmland and disturbed forest around the edges (Saj et al. 2005).

Study groups

This study compared one group of *C. lowei* (Fig. 2) that consistently receives a high level of provisioning by visitors/tour guides as they range within the interconnecting trails in the sanctuary (referred hereinafter, for simplicity, as the high-level provisioning group [HP group]), and another group that had low levels of provisioning by visitors/tour guides and do not range within the tourist trails in the sanctuary (referred hereinafter, for simplicity, as the LP group).

The HP group consisted of 32 individuals in total—one adult male, 13 non-lactating females, two adult females with infants, and 16 young animals.

Fig. 2. *Cercopithecus lowei* (adult female).

Their range is divided by wide routes where inhabitants of Boabeng come and go from their farms, and these paths are also used for tour guides to easily find the monkeys during their tours. This group spent most of their time around the paths used by tour guides in the sanctuary, where they frequently get hand-fed almost daily by visitors and tour guides with a variety of foods (*e.g.*, banana, apple, coconut, bread, biscuits, peanuts). The group occasionally steals foodstuffs from farmers on their way home from the farm, and also enter people's homes to take cultivated foods such as yam, cassava, corn, palm nuts, and pineapple. The group also forage around corn milling machines (Fig. 3) and refuse dump areas. Herein visitors are understood as people (international or national) who travel to BFMS and tour the area, whether they interact (*i.e.*, feeding or calling) with the monkeys or not (*i.e.*, watching or photographing).

The LP group was made up of 34 individuals—two adult males, seven non-lactating females, four females with infants, and 21 young animals. This group does not come close to humans (visitors or tour guides) as their daily range is not close to the tourist feeding paths, they had less interaction with humans, and thus a four-week habituation period was needed to start data collection. There was no fecundity or mortality in either of the two groups during the study period. It took four weeks to habituate the LP study group. The habituation consisted of daily walks through the LP group range, progressively increasing the proximity to the group to finally follow them from a distance (*i.e.*, 30–50 m) without the group fleeing or moving deeper into the forest. They fed largely on natural foods, and eventually supplemented their diet with cultivated foods (*e.g.*, yam, cassava, corn) from the farmer's barns closer to the edge of the forest during the farming season. The group were not provisioned by visitors or tour guides during this study. Both monkey groups traversed the core forest where the vegetation consisted of open and closed forest and savannah woodland, although there was no overlap between their ranges. The two groups were not seen interact with other *C. lowei* groups at the site during the study period.

Data collection

Research was conducted from January to March 2014 during the dry season and from May to July 2014 during the wet season to minimize seasonal bias, as monkeys' behavioral patterns vary throughout the year as a consequence of unstable food availability between seasons (Schubert 2011). The study was conducted in the core Boabeng-Fiema Monkey Sanctuary (Boabeng and Fiema communities), and did not include the entire

sanctuary with the associated surrounding communities forests. The behavioral data were obtained through daily observations from dawn to dusk (*i.e.*, ~ 0600 h to 1800 h). Each period of study (*i.e.*, dry and wet season), 20 full day follows per group were obtained, accounting for a total of 960 hours of observation. Each day, the data collecting period was blocked into two 6-hour sessions (*i.e.*, 0600–1200 h and 1200–1800 h) to allow two researchers to alternate between morning and afternoon sessions, and HP/LP group follows were alternated weekly. An inter-observer reliability test was done before starting the study and during it. Observers showed scores above 90% agreement. Prior to following a focal group, the group was followed in the evening until they were settled in their sleeping tree so that the next day they could be located at sunrise.

The HP and LP groups were distinguished by identifying at least seven individuals within the groups without a doubt (Table 1). To ensure that the same group was selected for the study daily, it was essential to identify at least three individuals in the group before starting observations. The study adopted an age-sex classification (Table 2) as defined and used by Porter (2005). To record the behaviors of the monkeys, successions of 15-minute scan samplings and 10-minute agonism-focal samplings were performed (Altmann 1974). The following information was collected during scans—time, age and sex of the animal sampled; activity in which the animal was engaged at the moment of the scan (categories are described on

Fig. 3. *Cercopithecus lowei* high-level provisioned group being fed by a group of tourists in the forest (top); foraging around corn milling machine (bottom) in Boabeng community.

Table 3); the canopy level of the tree (stratum) where the monkeys were located; and the number of visitors in proximity (within 20 m) to the focal group. Four stratum categories were described: Ground, at least two limbs of the animal are on the forest floor; Low, when both limbs are above the ground but not higher than 3 m; Medium, the animal is between three and ten metres above ground level; and High, when the animal is more than 10 m above ground level (Porter 2005). Age-sex class was applied as defined and used by Porter (2005). For each group, five individuals were chosen randomly for each scan (*i.e.*, select an individual within a group by chance and note all behaviors of interest for a given period). The scans were done from the right to left of the group in an interval of no more than 5 minutes; one lasted for > 5 minutes and was not considered in the data analysis. Efforts were also made not to scan individuals twice consecutively in order to have a better representation of all individuals in the group. Only activities lasting a minimum of 5 seconds without interruption (*i.e.*, without the animal changing to another activity) were recorded. The scan sampling method was used to assess the approximate percentage of time that Lowe's monkeys spent for each activity. During feeding, food items eaten (*i.e.*, leaf, fruit, seed, flower, stem, or insects) were recorded, which also included human-food types (*e.g.*, corn, banana, groundnut, pineapple, yam, cassava, coconut).

Agonistic behaviors were recorded between scans during the 10-minute agonism-focal sampling. Agonistic acts are event behaviors, unlikely to be recorded in scans; we therefore needed to do agonism

Table 1. Identity of some individuals within the High-level provisioning group and Low-level provisioning group in the Boabeng-Fiema Monkey Sanctuary

Group	Name	Age-Sex Category	Characteristics
HP group	Spotty	Adult female with infant	- Normally holding infant - One white spot on each side of its nose
	Alfa	Adult male	- Bigger than females - Big scar on its right leg - Slim face compared to other males
	Lisi	Adult female	- Short tail - Many spots in its face
	Torta	Adult female	- Tail ending in a hook-shaped
	Zig-zag	Adult female	- Tail shaped with light zigzag
	Aye	Adult female	- Wart on its right eye
	Pequito	Immature animal	- Warts on its nose and eyes
LP group	Big	Adult male	- Big body size
	Peke	Adult male	- Small head - Small body
	Turnhead	Adult female	- Head turned to the right side
	Coil	Adult female	- Coiled tail
	Goofie	Adult female	- Puffy tail
	Blanki	Adult female	- Black nipples
	Pirate	Adult female	- Only had one eye
	Baby	Adult female	- Smallest female

Table 2. Criteria used for age-sex identification in *C. lowei* (Porter 2005)

Age-Sex Categories	Description
Adult Female	Pendulous, elongated nipples (due to nursing) Breast area often enlarged
Adult Male	Enlarged, fully descended, blue-colored testes Approximately 30-40% larger than most adult females
Adult Female with Infant	An adult female with infant clinging and/or suckling
Immature animal	Immature females: small, short nipples Immature males: small testes located close to the body

focals to get accurate data on agonism rates in each group. Once the scan was over, we began a focal-animal sample on an adult animal. The following data was collected in each 10-minute agonism-focal sample – observation time, age-sex class of the animal sampled; time when an agonistic behavior started and ended; the actor and recipient of the agonistic action; and if visitors were in close proximity (*i.e.*, within 20 m) and interacting with the focal animal (*i.e.*, offering food, calling, or photographing). The next focal individual was chosen as the closest adult that was on sight and had not been sampled during the two previous scans. If no adult animal was visible or if the sighting had already been recorded, the focal sampling was skipped for that interval. Agonism focals were discarded if the subject moved out of the visibility area for more than 3 minutes. The agonistic categories recorded were chase (when one individual follows another involving one or more gesticulations and ending with any violent or submissive outcome), threat (any aggressive sign from one animal towards the other, including staring with tense body, open-jawed gaze gesture or head-bobbing), and attack (when two individuals were mutually hitting, grabbing or biting).

Full day follows (*i.e.*, 0600 h to 1800 h) were also used to measure the daily path length (Radhakrishna and Singh 2002) and daily distance travelled (Kaplin 2001). The area traversed by the study groups during the routine daily activities (Kaplin 2001) was mapped with a Garmin 60CS Global Positioning System (GPS). The location of the focal group (distance travel) was recorded every 30 minutes by standing at the approximated centre point of the focal group with a GPS with a single digit as an acceptable error margin.

Statistical analyses

The number of behavior occurrences collected during scans was 9,646 and 10,118 for the HP group and LP group, respectively (totalling N = 19,764). After cleaning the database, the number of scan observations used for the analysis was 8,732 for the HP group and 9,293 for the LP group (N = 18,025).

The primary behavioral analyses and the evaluation of the influence of explanatory variables were carried out using Generalized Linear Models (for percentages or counts), in which the date were considered as a random factor. In order to run these analyses, it was assumed that the selection of subjects was random because they were drawn from larger groups to make the sample more representative and less biased. A model was run for each behavior in the activity budget (scans data), and another for each agonistic behavior (agonism-focal data). The response variables considered for each independent behavior were feeding, resting, moving, or socializing, while those for each agonistic behavior were threats, attacks, chases, or all actions. The explanatory variables considered for both models were the focal group, visitors' numbers, age and sex of the monkeys (*i.e.*, adult male, adult females, adult females with infant and juveniles), time of the day, and weather conditions. The aggregated data for each hour were used as an experimental unit. The measurements for agonistic behavior were aggregated and analysed at a day level due to the small number of aggressive behaviors. A Chi-square test was used to analyse the differences in diet between within the two monkey groups. The Tukey HSD (Honest Significant Differences) was carried out to find which of the groups differed in variance. Daily-journey length (distance travelled per day) was estimated from the distance covered from the previous sleeping site (with 30 minutes GPS points) to where the group ended up sleeping that day (Muroyama et al. 2000). Home ranges were generated and estimated from the locations recorded with the GPS device using the Kernel Density

Table 3. Ethogram (Porter 2005)

Ethogram behavior	Description
Feed	Included feeding, food handling and foraging
	Foraging included all search behavior, such as
	- Scanning substrates *i.e.*, leaves, bark, etc. (or the refuse deposit) for food
	- Handling leaves to search for plant or prey foods
	- Moving as it searched for food items
	Feeding from cheek pouches while sitting
Rest	Animal was stationary in a standing, sitting or lying position
	No chewing (*i.e.*, feeding) or socializing was occurring
Move	Included all possible ways an animal might move through the forest, such as walking, running, swinging, jumping, etc.
Social	Affiliated and agonistic behaviors included displacements, chasing, biting, grabbing, or any other aggressive behavior, all of which occurred in an agonistic context (distinct from a play context)

Estimation method (Laver and Kelly 2008). The area of the monkey's home range was calculated using the Continuous-Time Movement Modelling (ctmm) R package. The daily distances travelled and speeds were calculated using the software R (version 3.1). A total of 1621 points were used for the analysis, 651 for HP group and 970 for LP group. A *t*-test was used to compare the daily distance travelled between the HP and LP groups. All other statistical analyses were run with the software SAS System version 9.3 and statistical significance was set at $p < 0.05$ unless stated otherwise.

RESULTS

General activity pattern

The HP group spent on average 33.74% of their time resting, followed by moving (28.06%), feeding (24.87%) and socializing (13.33%) (*i.e.*, Rest > Move > Feed > Social). The LP group showed similar results in their activity budget: time resting (36.16%), moving (30.22%), feeding (29.62%) and socializing (4.00%) (Fig. 4). Results showed a significant reduction in movement in the HP group (*d.f.* = 76, F = 15.19, $p < 0.001$), especially in the afternoon across age-sex categories and increased socializing throughout the day (*d.f.* = 76, F = 42.56, $p < 0.001$). Rest and feed did not show significant differences between groups (rest: *d.f.* = 76, F = 0.95, $p = 0.333$; feed: *d.f.* = 76, F = 2.44, $p = 0.122$); however, the HP group significantly fed less and rest more than the LP group (*d.f.* = 17907, F = 4.24, $p < 0.001$). Females in the HP group also significantly fed less (*d.f.* = 17907, F = 9.03, $p = 0.003$) and rested more (*d.f.* = 17907, F = 6.64, $p = 0.010$); whereas females with infants also spent less time feeding in the HP group than those in the LP group (*d.f.* = 17907, F = 15.66, $p < 0.001$).

Activity patterns in the presence of visitors

In the presence of visitors, the HP group significantly increased the time spent feeding (*d.f.* = 8672, F = 27.83, $p < 0.001$), and significantly decreased their time resting (*d.f.* = 8672, F = 5.65, $p < 0.001$). No significant differences were recorded for moving (*d.f.* = 8672, F = 2.22, $p = 0.109$), and socializing (*d.f.* = 8672, F = 2.27, $p = 0.103$), either in the presence of small (*i.e.*, 1–10 visitors) or big groups of visitors (*i.e.*, > 10 visitors).

Diet

A total of 4,924 feeding observations were made: 2,173 feeding observations for the HP group and 2,751 feeding observations for the LP group. There was a significant difference in diet between the two groups ($\chi^2 = 566.34$, $p < 0.001$). Post-hoc Tukey HSD test showed a significant difference between combinations of food items except for water (Tukey's test: $p < 0.001$;

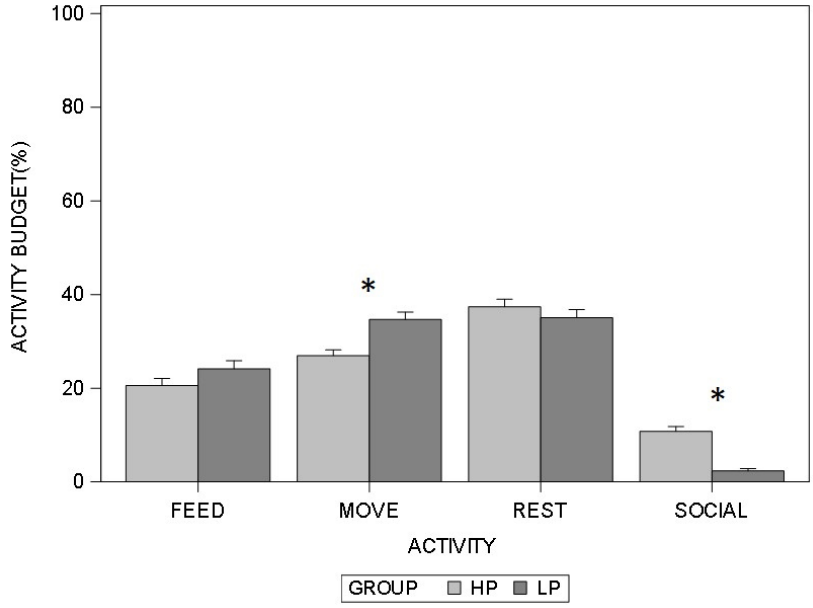

Fig. 4. Comparison of mean proportion of scans allocated to feeding, moving, resting, and social activity between a group high-level provisioning group (High-level provisioning group – light grey) and a low-level provisioning group of *C. lowei* (Low-level provisioning group – dark grey). (Error bars indicate SE; * significant differences at $p < 0.05$).

Table 4). The LP group fed more on fruits (24.2%) and insects (44.9%), whereas the HP group largely (24.3%) depended on human food (*i.e.*, banana, corn, apple, pineapple, coconut, mango, palm nuts, peanuts, yam and cassava) and insects (33.10%) (Table 4).

Agonistic behaviour

The rate of aggression for both groups was low, both when visitors were present and absent. For overall actions (*i.e.*, threat, chase, and attack), there was a significant difference between groups (*d.f.* = 45, F = 26.00; $p < 0.001$).

For the HP group, 3.5% of the events during the overall agonism-focal time were agonistic behaviors, the most of which were threats, followed by chases and attacks. Threats were significantly more frequent (*d.f.* = 45, F = 17.18, $p < 0.001$), but there was no significant difference between them and attacks (*d.f.* = 45, F = 0.00, $p = 0.973$) or chases (*d.f.* = 45, F = 2.01, $p = 0.163$).

The LP group showed agonistic behavior 1.15% of the sampled time; chasing was the most common, followed by threats and attacks.

Visitor's presence and aggressions

Aggressive behaviors of the HP group significantly increased when visitors were around (*d.f.* = 19, F = 11.87, $p < 0.001$). Larger visitors' numbers increased aggression even more. The percentage of aggressive behavior was 12.81% when no visitors were around; however, this increased to 30.18% when one to fifty visitors were present. Where more than 50 visitors were present, the aggression rate increased to 57.01%. No significant differences were found for any specific agonistic behavior (*i.e.*, threats, attacks, chases) when analysed separately.

Daily distance travelled and home range

The *C. lowei* HP group travelled significantly less (*d.f.* = 68, F = 51.17, $p < 0.001$), 0.88 km daily on average, and had a smaller home range size (4.68 ha) (Fig. 5). They spent most of their time in and at the edge of the village raiding people's houses for human food (*e.g.*, yam, cassava, corn, palm nuts, pineapple) and being around visitors or tourists when they were present. Their home range varied in size during the two periods: during the dry season, their home range was bigger (4.99 ha) than during the wet season (4.36 ha) (Fig. 5).

The LP group travelled 1.4 km daily on average and their home range was relatively bigger (14.25 ha) (Fig. 4). They spent most of their time in the forested area, but they also moved around a few human settlements (*i.e.*, houses, church, roadside). Similar to the HP group, the LP group's home range was bigger during the dry season (17.34 ha) and smaller during the wet season (11.16 ha) (Fig. 5). Both the *C. lowei* HP and LP groups had little home range overlap with neighbouring groups.

Overall strata use

Generally, the *C. lowei* HP group spent significantly more time in the medium strata (*d.f.* = 76, F = 7.60, $p = 0.007$) than the *C. lowei* LP group (Fig. 6). However, the time spent in the high, low, and ground strata was not significantly different between groups (ground: *d.f.* = 76, F = 0.33, $p = 0.567$; low: *d.f.* = 76, F = 2.59, $p = 0.112$; high: *d.f.* = 76, F = 2.05, $p = 0.157$).

Specifically, we found significant differences in the use of each stratum between groups depending on the time of the day (ground: *d.f.* = 76, F = 4.24, $p < 0.001$; low: *d.f.* = 76, F = 6.57, $p < 0.001$; medium: *d.f.* = 76,

Table 4. Percentage of food eaten by groups with high and low levels provisioning by visitors at BFMS. Post-hoc Tukey HSD tests showed a significant difference between combination of food items except for water. The last column shows the level of significance (*: $p < 0.05$, **: $p < 0.01$ and ***: $p < 0.001$)

Item eaten	High-level provisioning group (%)	Low-level provisioning group (%)	*P* value
Flowers	1.80	0.91	**
Fruit	13.17	24.23	***
Human food	24.26	10.39	***
Insects	33.10	44.93	***
Unknown*	18.37	15.15	***
Seeds	0.09	3.60	***
Stems	1.84	0.36	***
Water	0.32	0.44	0.629

*Unknown food refers to items that were eaten by the monkeys but the exact nature could not be determined either due to its small size or poor visibility.

F = 2.69, $p = 0.001$; high: *d.f.* = 76, F = 7.92, $p < 0.001$), mainly during the afternoon hours. The HP group used the medium stratum more and the low and high strata less compared to the LP group (Table 5).

Age and sex also had a significant influence on the use of ground strata (*d.f.* = 17694, F = 20.02, $p < 0.001$), low (*d.f.* = 17694, F = 2.83, $p < 0.037$), and high (*d.f.* = 17694, F = 8.96, $p < 0.001$). Males and females, in

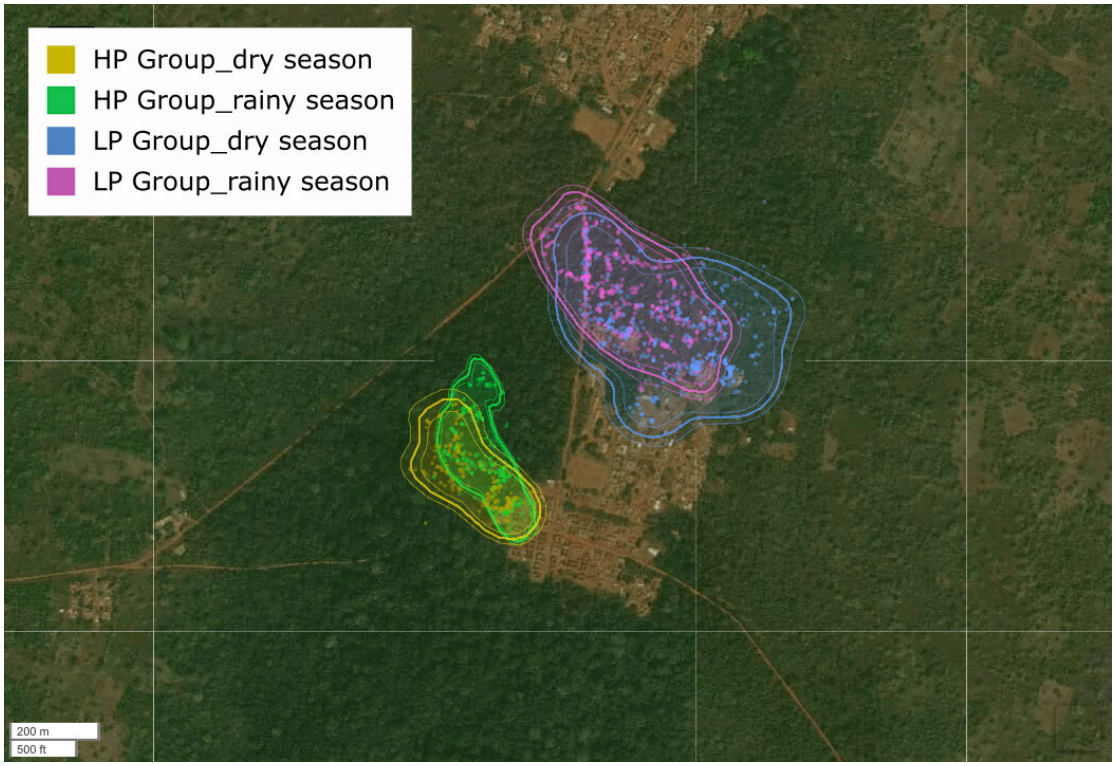

Fig. 5. Variation in *C. lowei* home range size for high-level provisioned group (High-level provisioning group) and low-level provisioned group (Low-level provisioning group) in dry and wet season at the Boabeng-Fiema monkey sanctuary. (Home range sizes – HP group: dry season, 4.99 ha; rainy season, 4.36 ha; LP group: dry season, 17.34 ha; rainy season, 11.16 ha).

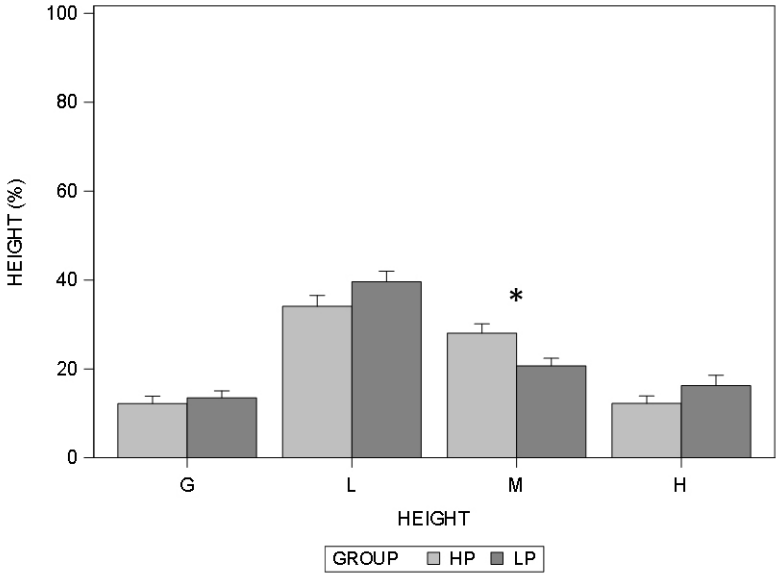

Fig. 6. Comparison of the proportion of time spent in each stratum level (ground, low, medium, high) by the high-level provisioning group (light grey) and low-level provisioning group (dark grey) of *C. lowei* in the BFMS. (Error bars indicate Standard Error; * significant differences at $p < 0.05$).

the HP group used the high canopy less (males: *d.f.* = 17907, F = 4.84, p = 0.028; females: *d.f.* = 17907, F = 6.71, p = 0.010), and females with infants spent less time in the low stratum (*d.f.* = 17907, F = 6.60, p = 0.010) compared to those in the LP group. Finally, in the HP group juveniles used the ground level less (*d.f.* = 17907, F = 5.51, p = 0.019) than males who spent more time in it (*d.f.* = 17907, F = 5.13, p = 0.024) compared to the LP group.

Strata use in the presence of visitors

The number of visitors present at a time significantly influenced the stratum used by the monkeys. When no visitors were present, *C. lowei* spent 12.57%, 28.21%, and 11.9% of their time in the low, medium, and high strata, respectively. In the presence of visitors, there was a significant increase for use of the ground strata (*d.f.* = 8672, F = 20.84, $p < 0.001$), and a significant decrease for medium strata (*d.f.* = 8672, F = 8.55, $p < 0.001$) and high (*d.f.* = 8539, F = 11.43, $p < 0.001$). There were no significant differences for the low strata (*d.f.* = 8672, F = 0.92, p = 0.398). The use of low strata increased by 18%, whereas the use of medium and high decreased by 13.90% and 10.12%, respectively, in the presence of one to ten visitors. The presence of more than 10 visitors did not significantly influence the use of strata by *C. lowei* when compared to the presence of fewer than 10 visitors (ground: t = 0.46, p = 0.642; low: t = -0.47, p = 0.638; medium: t = -1.10, p = 0.272; high: t = -0.37, p = 0.558).

Table 5. Comparison of the percentage of mean time spent on each stratum by high-level and low-level provisioning *C. lowei* groups in the Boabeng-Fiema Monkey Sanctuary at different hours of the day using Type III Test of Fixed Effects in Generalised Linear Models in SAS. The last column shows the level of significance (*: $p < 0.05$, **: $p < 0.01$ and ***: $p < 0.001$)

Source	Time of day (hour)	HP (%)	LP (%)	*F* value	*P* value
Ground					
Group*TOD	0700	42.98	10.67	4.46	*
	1500	13.14	28.26	11.4	***
Low strata					
Group*TOD	0600	11.37	23.80	30.24	***
	0700	27.85	34.07	11.42	**
	0800	40.63	41.71	4.16	*
	0900	43.52	51.18	9.46	**
	1000	49.50	56.89	8.03	**
	1100	47.41	56.54	9.16	**
	1800	35.26	12.50	8.16	**
Medium strata					
Group*TOD	0700	48.34	27.01	22.49	***
	0800	35.34	22.96	7.95	**
	0900	31.73	20.87	6.86	**
	1000	32.39	18.61	10.43	**
	1100	31.31	17.92	11.36	**
	1200	33.64	22.10	6.78	**
	1500	32.21	20.82	6.13	*
	1600	29.21	18.40	6.42	*
	1700	30.25	21.16	5.38	*
High strata					
Group*TOD	0600	51.61	46.91	7.05	**
	1200	6.75	15.38	5.48	*
	1300	4.48	10.91	4.63	*
	1600	7.69	18.74	6.89	**
	1700	10.29	21.91	8.88	**
	1800	20.00	50.56	14.54	**

DISCUSSION

Factors influencing the activity budget of Lowe's monkey

Resting was the main activity for both *C. lowei* study groups in the BFMS (HP group, 33.62%; LP group, 36.09%). The results for the HP group are similar to other studies in which provisioned groups of *Chlorocebus aethiops pygerythrus* (Saj et al. 1999), *Papio cynocephalus* (Altmann and Muruthi 1988) and *Cercopithecus aethiops* (Brenan et al. 1985) rest more than any other activity. Notably, the LP group in the BFMS also spent more time resting than feeding, unlike what was observed in other cercopithecines (*e.g.*, a troop of non-provisioned *P. cynocephalus* (Altmann and Muruthi 1988), and in a wild-feeding group of *Macaca sylvanus* (Alami et al. 2012)), possibly intermittent access to other high-energy food sources (*e.g.*, especially, foodstuffs from farmers' barns), which can help them to supplement their daily energy intake faster.

Comparatively, the LP group was likely to spend more time feeding (*i.e.*, foraging and food intake) than the HP group, but this was not significant. Previous activity budget studies showed that groups with high levels of provisioning spent less time foraging (Unwin and Smith 2010; Alami et al. 2012). Our findings are contrary to these observations, possibly because this study did not separate time spent foraging from time spent actually ingesting food. The feeding time for the LP group was relatively longer than the HP group because the latter may not need to spend time foraging in the forest, which is costly in terms of time (Brenan et al. 1985; Unwin and Smith 2010). The HP group may satisfy its metabolic needs faster (Saj et al. 1999) than the LP group by getting human food from the visitors or raiding houses in the village for food, which are generally high-energy.

The LP group spent significantly less time socializing and more time moving, as observed by other researchers (Altmann and Muruthi 1988; Brenan et al. 1985). It is likely that the LP group had to spend more time looking for resources to satisfy their metabolic needs, which is why they spent less time socializing. On the contrary, the HP group spent less time feeding and moving, which frees up time for socializing activities. They have been habituated to humans for a long time, live close to the community, and are fed by visitors, thus increasing the time the HP group has to socialize; this could be a way to reduce the stress caused by visitors' presence or interactions (Matheson et al. 2006). On many occasions, individuals within the HP group fought when they were being hand-fed by visitors.

When looking at the effect of the presence of visitors on the HP group, we found that, relative to when visitors were absent, the presence of visitors significantly increased the feeding time and reduced the resting time, especially during tours where the monkeys are hand-fed by visitors for a long time (Asquith 1989). In the BFMS, *C. lowei* feeds early in the morning and late in the afternoon, and rests in midday hours, matching the findings of Fargey (1991). This diurnal activity pattern was similar to that of the spider monkeys at Lago Caiman (Wallace 2001) and proboscis monkeys (Matsuda et al. 2009; Matsuda et al. 2014) in Sabah, Malaysia. In the BFMS, the monkeys do not forage actively whenever it is raining; some monkeys feed more in cloudy weather (Bronikowsky and Altman 1996; Wallace 2001).

Cercopithecus lowei in the BFMS feed more on insects (Porter 2005) than Campbell's guenon (*C. campbelli*) in the Taï Forest, Ivory Coast (Galat and Galat-Luong 1985; Buzzard 2006). Generally, the HP group depended more on human food while the LP group fed more on fruits and insects in the wild. On the contrary, in the BFMS, the HP *C. lowei* group does not eat more foliage than fruit (Porter 2005), even in this study. In 1991, Fargey (1991) observed that the average diet composition of three *C. lowei* groups in the BFMS consisted of 26.3% (range: 0–68.8%) food scraps thrown into refuse dumps. Since monkeys are social animals and can acquire behavior or knowledge through social interactions (Heyes 1994; Galef 1996; Heyes and Galef 1996; Galef and Giraldeau 2001), then it is possible that the *C. lowei* HP group could be a generation of those which largely depended on refuse 29 years ago in BFMS; confirming what has been observed in other matrilineal primate groups which show fidelity to their home range over many years (*e.g.*, Baboons at Amboseli National Park (Alberts and Altmann 2012) and grey-cheeked mangabeys at Kibale National Park (Janmaat et al. 2009).

Presence of visitors and agonistic behavior of Lowe's monkey

Agonistic behaviors were not frequent in the BFMS because food resources are so abundant (Knopff and Pavelka 2006). The agonistic behaviors mostly occurred during three different situations. First, intra-group individuals competed over clumped food resources, either in the village or when visitors fed the monkeys during their visits. More aggression was observed when the foods that were given to the monkeys by visitors were not enough to feed the whole group (Southwick et al. 1976). Second, the increase observed in aggressive behavior of the HP group when tourists are present may be because of the negative

behaviors of the tourists (*e.g.*, scaring the monkeys with a hand claps or other hand gestures) toward the monkey group when interacting with them, which is fed back to the interaction within the monkey group, or by the frequency of conflicts between monkeys and inhabitants from the village. Third, to defend the group's home range, the monkeys were involved in intergroup territorial fights. Fourth, the presence of babies in the group often leads to fighting or disputes between females who attempt to allomother infants (Badiella pers. obs.). This is consistent with the findings of Southwick et al. (1976) who observed that in Rhesus macaques (*Macaca mulatta*) there were increased aggressive interactions when food was being provided. The type of food, either preferred or non-preferred food, which primates are provided (Southwick et al. 1976; Mallapur et al. 2005) by visitors or tour guides and negative behaviors of visitors towards the primates may also influence the monkey group interactions. For example, on a few occasions, there were fights over preferred limited food resources (*e.g.*, a mango tree with few mangos on it), although that was very rare. There was also aggression when juveniles were fed or received more hand-fed food from visitors than adults in BFMS. The adults would then attack or chase the juveniles, who were presumably lower-ranking. Such behavior has been reported in *Macaca tibetana* (Matheson et al. 2006). In the LP group, food competition was minimal.

In the BFMS, when a monkey was holding food or eating close to another monkey of the same group, a threat or an attack was usually observed when the other monkey tried to get some of the food. It is indeed unusual for monkeys to eat close to one another (*i.e.*, co-feed, Brenan et al. 1985). We did not record any aggression from monkeys toward humans during the study; a monkey was observed to topple over a basin full of farm produce (*e.g.*, banana, palm nut, corn) from a farmer returning from the farm, but this incident happened before the actual data period for this survey. On different occasions, monkeys were also seen stealing food from a bag hanging from a visitor's hand, or from bags on the ground. On several occasions, inhabitants from the village were seen throwing small stones at the monkeys to scare them away and prevent them from entering their houses or barns. Adult monkeys were seen exposing their teeth to threaten visitors, especially whenever visiting school children had scared the monkeys. Two monkey bites were reported to the Wildlife Officer in charge of the sanctuary during this study. Also, Julie Teichroeb saw a visitor been bitten by a *C. lowei* monkey in a process of feeding it during her research at the site (pers. com.).

Home range and daily distance travelled

The abundance and easy accessibility of food from visitors influenced the ranging patterns of *C. lowei* in BFMS (Wallace 2008; Alami et al. 2012). The home range size for *C. lowei* HP group was smaller (4.68 ha) than that with the low level of provisioning by visitors (14.25 ha). Access to alternate foods from visitors (*e.g.*, bread, biscuits, apple, coconut, peanuts) which are possibly high in calories (Fa 1986) and time spent waiting for visitors to show up in the village might have restricted their time searching for natural foods, hence leading to a reduction in the home range and daily distances travelled by the *C. lowei* HP group. This group also visits the Boabeng community frequently, even if there are no visitors to feed them. They have become habituated to humans and appear to prefer this easy food source although they are free-ranging monkeys in a natural forest. Most transects used as tour routes are placed in the core forest area where tourists or visitors congregate. The visitors use food as an attractant to get closer to the monkeys and feed them with artificial food, thereby causing them to reduce their home range size and daily travel distance (Asquith 1989). In the absence of visitors, the monkeys move from the core forest to the Boabeng community in the morning to look for food in houses and food barns. They go back into the forest by midday and return in the evening to look for food in the community before dusk. On the other hand, the *C. lowei* LP group travelled more and may have explored new areas (expanded their home range) possibly to find more specialized natural food resources (Marsh et al. 1987; Saj et al. 1999), as observed in other monkeys, for example, *Macaca Sylvanus* (Unwin and Smith 2010; Alami et al. 2012) and *Chlorocebus aethiops pygerthrus* (Saj et al. 1999). Also, when food resources are scarce, primates might increase their search time for food, thereby increasing their home range (Marsh et al. 1987).

Strata use

Strata use corresponds to food availability and accessibility in most primates (Glenn 1996; Siemers 2000). In the BFMS, the long-term provisioning makes primates associate visitors to food, encouraging the primates to approach the visitors anytime they are around, therefore increasing the use of ground and reducing high and medium strata use. When visitors were around the core forest area, the HP monkey group often descend to the ground and approach the visitors to get food from them. When the number of visitors increased to more than 10 visitors, the monkey group then moved into the medium strata to avoid direct contact with humans (de la Torre et al. 2000) as reported

elsewhere (Fleagle et al. 1981; Terborgh 1983; McGraw 1996; Porter 2005; Buzzard 2006), to explore if they could be given any food by the visitors.

The most used strata for *C. lowei* in the BFMS were low and medium for both groups. Medium stratum was used mainly for social activities in both groups which brought the differences in the use of canopy levels, as the LP group spent less time on social activities. However, the LP group travelled more on the ground and low strata compared to the HP group, which used lower and medium strata. This may be a result of their home range being more fragmented than that of the HP group, as observed in *Chlorocebus djamdjamensis* when moving across fragmented forest patches with fewer trees (Mekonnen et al. 2018). Similar to Peignot et al. (1999), the use of high stratum was observed most by adult males followed by adult females when resting. Adult males from the LP group also tend to use less the ground and more the high stratum than those in the HP group. The use of the high strata especially by adult males may signal to the other group members that there is danger present (Bourliere et al. 1970; Porter 2005) or be an attempt at extra group mating activities (Gautier-Hion 1980).

CONCLUSIONS

This study revealed that high levels of provisioning by humans was found to affect the activity budget, diet, and range and strata use in the population of Lowe's monkeys in the BFMS. Uncontrolled provisioning of primates may result in controversial situations for both actors alike, humans and primates. As proved in this study, long-term provisioned primates tend to rely on the food provided and become aggressive towards the source of interest to the monkey, mainly humans with food (*e.g.*, in Gibraltar macaques: Radford et al. 2017, Formosan Macaques: Hsu et al. 2009).

Feeding the monkeys could affect the natural behavior of the monkeys and increase the raiding behavior of the monkeys in the villages, thereby creating serious human-wildlife conflict in the area. The people of the BFMS have greater respect and reverence for the black and white colobus because they do not raid the village for food, but they often express frustration and disdain for the Lowe's monkeys (Saj et al. 2005). This leads to a situation where the Lowe's monkeys could be harmed, despite their sacred status at the site.

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