PRIMATOLOGY WILEY

Influence of rainfall on sleeping site choice by a group of anubis baboons (*Papio anubis*)

Alexandre Suire[1,2] | Lynne A. Isbell[2,3,4] | Laura R. Bidner[2,3,5] |
Yushin Shinoda[6] | Munemitsu Akasaka[6,7] | Akiko Matsumoto-Oda[2,8]

[1]Faculty of Global and Regional Studies, University of the Ryukyus, Okinawa, Japan

[2]Mpala Research Centre, Nanyuki, Kenya

[3]Department of Anthropology, University of California, Davis, California, USA

[4]Animal Behavior Graduate Group, University of California, Davis, California, USA

[5]School of Human Evolution and Social Change, Arizona State University, Tempe, Arizona, USA

[6]Institute of Agriculture, Tokyo University of Agriculture and Technology, Tokyo, Japan

[7]Institute of Global Innovation Research, Tokyo University of Agriculture and Technology, Tokyo, Japan

[8]Graduate School of Tourism Sciences, University of the Ryukyus, Okinawa, Japan

Correspondence
Akiko Matsumoto-Oda, Graduate School of Tourism Sciences, University of the Ryukyus, 1 Senbaru, Nishihara, Okinawa 903-0213, Japan.
Email: a_matsu@grs.u-ryukyu.ac.jp

Abstract

For diurnal nonhuman primates, shifting among different sleeping sites may provide multiple benefits such as better protection from predators, reduced risk of parasitic infection, and closer proximity to spatially and temporally heterogeneous food and water. This last benefit may be particularly important in sleeping site selection by primates living in savanna-woodlands where rainfall is more limited and more seasonally pronounced than in rainforests. Here, we examined the influence of rainfall, a factor that affects food and water availability, on the use of sleeping sites by anubis baboons (*Papio anubis*) over two 13-month study periods that differed in rainfall patterns. We predicted that during wet periods, when food and water availability should be higher, the study group would limit the number of sleeping sites and would stay at each one for more consecutive nights than during dry periods. Conversely, we predicted that during dry periods the group would increase the number of sleeping sites and stay at each one for fewer consecutive nights as they searched more widely for food and water. We also predicted that the group would more often choose sleeping sites closer to the center of the area used during daytime (between 07:00 and 19:00) during wet months than during dry months. Using Global Positioning System data from collared individuals, we found that our first prediction was not supported on either monthly or yearly timescales, although past monthly rainfall predicted the use of the main sleeping site in the second study period. Our second prediction was supported only on a yearly timescale. This study suggests that baboons' choice of sleeping sites is fluid over time while being sensitive to local environmental conditions, one of which may be rainfall.

KEYWORDS
baboons, rainfall, savanna, seasonality, sleeping site

1 | INTRODUCTION

In many primate species, groups generally exhibit a preference for a few sleeping sites while occasionally shifting to other sleeping sites that are used more rarely (Chapman, 1989; Hamilton, 1982; Hausfater & Meade, 1982; Holmes et al., 2011; Markham, Alberts et al., 2016; Markham, Guttal, et al., 2013). The use of multiple sleeping sites and of shifting among them may be related to inter-group competition for resources that shape space-use strategies (Markham, Guttal, et al., 2013) but variable sleeping site use may also have multiple benefits. First, it may weaken the ability of predators to locate their primate prey (Hamilton, 1982). Second, it may

help reduce the risk of parasitic infection as fecal matter accumulates over time at sleeping sites (Hausfater & Meade, 1982). Third, it may provide more efficient access to food and water resources that are spatially heterogenous in the environment (Chapman, 1989; Von Hippel, 1998) as well as temporally variable, particularly for primates living in arid and semi-arid environments with very pronounced wet and dry seasons (Alberts et al., 2005).

In highly seasonal environments, food and water typically increase in availability during wet periods and decrease during dry periods, and dry periods may also force animals to prioritize access to water over food as water becomes more limited or localized (Altmann & Altmann, 1970; Chapman, 1989). Primates can respond to food scarcity in dry seasons by shifting to food resources that are abundant but have low profitability (e.g., "fallback foods"; Malenky & Wrangham, 1994; Wrangham et al., 1998) and/or track a relatively large number of different types of food over the year and selectively exploit them as they become available (Alberts et al., 2005). Primates may also use different tactics to access water during dry seasons, such as adjusting the frequency of trips to waterpoints or centering their activities around them (Chapman, 1988; Scholz & Kappeler, 2004). As a general consequence of marked seasonality, most studies have shown that primates living in such habitats often increase their day range length and foraging time during dry periods to maintain a relatively stable diet and/or meet important physiological water requirements (Alberts et al., 2005; Barton et al., 1992; Gursky, 2000; Overdorff, 1996; Post, 1981; Strier, 1991; but see Matsumoto-Oda & Palombit, 2015 for an absence of difference between wet and dry seasons in anubis baboons [Papio anubis] and Schreier, 2009 for a study showing that hamadryas baboons [P. hamadryas] travel longer distances during wet seasons).

In this context, one possible strategy for primates to mitigate these travel costs and efficiently exploit food and water resources across seasons is to adjust the use of sleeping sites distributed in their home ranges. With the expectation that individuals attempt to minimize costs in time and energy devoted to travel, one might predict that in arid and semi-arid environments, for example, savannas, savanna-woodlands, and bushed woodlands, primates will generally choose sleeping sites that are close to food and water resources. Therefore, they may need to minimize the number of sleeping sites they use and stay for more consecutive nights at each one during wet periods when resource availability is increasing, and, conversely, expand the number of sleeping sites they use and switch more frequently during dry periods to search for and exploit scarce or limited resources. As a consequence, one might also predict that primates living in such environments will more often choose sleeping sites closest to where they were active during the day during wet periods compared to dry periods. These predictions rest on the assumption that during wet seasons, primates may not need to travel far and/or switch to other sleeping sites as frequently because nearby replenished resources can be exploited for longer time periods. In contrast, during dry periods primates may need to increase their day range length to search for and exploit resources that are more temporally limited, thus more frequently switching to other sleeping sites.

Although a few studies have stressed the importance of the spatio-temporal distribution of food and water resources (Barton et al., 1992; Markham et al., 2013; Pontes & Soares, 2005; Teichroeb et al., 2012; Wang et al., 2011), to our knowledge no studies have investigated if patterns of sleeping site use track rainfall seasonality.

"Savanna" baboons (anubis, Guinea [P. papio], yellow [P. cynocephalus], and chacma [P. ursinus] baboons) are relevant for studying such questions as most live in semi-arid, highly seasonal, environments. They exhibit a flexible omnivorous diet, complex, variable social organizations and mating systems, and a high degree of behavioral plasticity (Alberts & Altmann, 2006, 1970; Barrett, 2009; Hill & Dunbar, 2002; Whiten et al., 1991). For savanna baboons, environmental seasonality has important consequences since rainfall has been found to affect the available biomass of their foods (Barton, 1990), the composition of their diet, and their foraging behavior (Hill & Dunbar, 2002). Indeed, studies have found that baboons increase their day range length and foraging time during dry seasons, possibly because they need to exploit foods that are more widely available but have lower nutrient value (Barton et al., 1992; Post, 1981). Another study further reported that baboons exploited and tracked different types of food over the year as they became available, which ultimately depended on rainfall patterns to renew seasonal foods such as fruits (Alberts et al., 2005). Moreover, it seems that the ranging patterns of a group may also be constrained by the availability of waterpoints, especially during dry seasons when temperatures rise, which in turn may determine sleeping site choice (Barton et al., 1992). In a broader context, it has been suggested that sleeping site use in baboons may be influenced by nearby foraging opportunities (Markham et al., 2016). Thus, one can reasonably expect rainfall seasonality to influence their sleeping site use.

In this context, the purpose of this study is to investigate the effects of variation in rainfall and the area used during daytime hours on an anubis baboon group's sleeping site choice, with a particular focus on their main sleeping site, on both monthly and yearly time-scales over two 13-month study periods. Anubis baboons live in large, cohesive, multimale, multifemale groups in semi-arid environments that range from savannas with the least amount of woody vegetation to savanna-woodlands and bushed woodlands with intermediate and more woody vegetation, respectively, from western to eastern Africa (Palombit, 2013). In these environments, anubis baboons tend to use as sleeping sites either cliffsides consisting of rocky ledges or faces of cliffs, or rocky outcroppings ("kopjes"), and riverine sites with relatively tall trees, in particular, Acacia xanthophloea, as sleeping sites. Cliffsides and kopjes are generally preferred over riverine sites (Bidner et al., 2018). We predicted that in the study period in which there was low and unmarked variation in rainfall, the group would switch sleeping sites more often than in the study period with more marked variation. We also predicted that the group would switch sleeping sites less often and stay for more consecutive nights at each site during wet months than during dry months. Finally, we predicted that the group would choose the closest sleeping site to the area they used during the day more often in wet months than in dry months.

2 | METHODS

2.1 | Ethics statement

The field research was approved by the Kenya governmental agencies National Council for Science and Technology (permit No. NCST/PRI/12/1/BS/240), National Commission for Science, Technology and Innovation (NACOSTI P16/84320/12475 and P/15/5820/4650). All research described here was approved by the Kenya Wildlife Service (KWS/BRM/5001) and adhered to the American Society of Primatologists Principles for the Ethical Treatment of Non-Human Primates. The research that began in 2014 was based out of the United States and conducted under University of California, Davis, IACUC protocol #17477. The research that began in 2016 was based out of Japan, which has no comparable approval process but is nonetheless compliant with the Japan Primate Society's "Guiding Principles for Animal Experiments Using Nonhuman Primates."

2.2 | Study site and subjects

This study was conducted during two periods, from January 19, 2014 to January 15, 2015 and from January 1, 2016 to January 31, 2017 (henceforth referred to as 2014 and 2016 study periods), at Mpala Research Centre (0°20'N, 36°50'E), a working cattle ranch and wildlife reserve on the Laikipia Plateau, Kenya. The surrounding environment includes bushed woodlands and riverine woodlands dominated by Acacia spp. (for more details on the study site, see Isbell et al., 2018).

The "AI" baboon group has been observed since 2011 and consisted of 51–62 individuals in the 2014 study period and 50–59 individuals in the 2016 study period. We based our analyses of sleeping site selection and group movements on the movements of a small number of adult females as representatives of their group since anubis baboons live in cohesive groups and females are philopatric (Barton et al., 1996). In keeping with the standards of ethical field research, we limited deployment of Global Positioning System (GPS) collars to as few individuals as possible to achieve our goals. Thus, collars were deployed on two adult females in 2014 and one adult female in 2016. GPS data suggest that they were indeed spatially well integrated with the group. In 2014, the two females were fairly cohesive, being located, on average, 40 m from each other (SD ± 60 m, median = 23 m, N = 22128) during the 10 months when both collars were functioning. Field observations across years also indicated that all collared females were socially well integrated into the group as they were always found with the rest of the group during morning censuses at the sleeping sites.

In 2014, after habituating the baboons to cage traps, two adult females were captured in cage traps and immobilized with 10 mg/kg ketamine hydrochloride (Agrar Holland BV) via intramuscular injection from a blowpipe. During collar removal, they were given ketamine and medetomidine hydrochloride (0.04 mg/kg; Pfizer Laboratories [Pty] Ltd.) to immobilize them using a blowpipe if they could be recaptured and a darting rifle if they remained free-ranging, and then the reversal agent atipamezole hydrochloride (0.1 mg/kg; Kyron Laboratories [Pty] Ltd.). The collars weighed approximately 450 g and included a GPS unit, an accelerometer data logger, and a D-sized-sized battery (Savannah Tracking, Inc.). As the females weighed 9.5 and 12.3 kg, both collars were 3.6%–4.7% of the animals' body mass, within the American Society of Mammalogists' guidelines of a maximum of 5%–10% of body mass (Sikes & the Animal Care and Use Committee of the American Society of Mammalogists, 2016). See Isbell et al. (2019) for more details. In 2016, the procedures were similar. The G5C-275F Solar GPS iridium collar (weight 465 g, SIRTRAC Ltd.) was attached to a different female weighing 16.0 kg by the same veterinarian who removed the collars in 2014.

Since one of the GPS collars stopped working during the 2014 study period, we analyzed only the locations of the other collar. We used a time interval of 1 h between GPS fixes for statistical analyses.

2.3 | Rainfall seasonality

The climate of the study site is characterized by a rotation of wet and dry seasons throughout the year. Wet seasons correspond to times of the year when most of the region's average annual rainfall generally occurs. Although the latter can be quite variable across years, Mpala generally experiences a trimodal pattern of wet seasons: long rains from April to May, short rains in November and an additional set of rains in July and August (Rubenstein, 2011). Months that are part of the wet seasons are called wet months. In contrast, the dry seasons are the yearly periods of low rainfall occurring between each wet season. Months that are part of the dry seasons are called dry months. For our analyses, we used rainfall and temperature data collected by the Mpala Research Centre staff. Since only 26 months of rainfall were analyzed here, which gives us a relatively small sample size (N = 26 months), we dichotomized wet months and dry months based on rules defined by Walter and Lieth (1960) and modified by Herrmann and Mohr (2011). They defined wet months as those with a total precipitation of more than two times the average monthly temperature, dry months within wet seasons as those with a total precipitation more than two but less than four times the average monthly temperature, and arid months with a total precipitation below two times the average monthly temperature and thus more extreme than dry months. Here, we calculated average monthly temperatures by first averaging daily temperatures from temperatures collected each hour at the Mpala Research Centre for each 24-h period, then averaging all daily temperatures. The threshold of four times the average monthly temperature for dry months within wet seasons "corresponds to the often-cited monthly rainfall threshold of 100 mm, below which water requirements for many crops are not satisfied and annual grasses with their short root systems suffer water stress" (Herrmann & Mohr, 2011), which should directly influence the availability of food resources for baboons.

2.4 | Sleeping sites

We identified sleeping sites based on clusters of GPS locations within the hours of 18:00 and 05:45 using Google Earth Pro v. 7.1.5.1557 (see methods in Bidner et al., 2018).

Occupancy of sleeping sites for every night was determined by the GPS fixes of collared individuals at 23:00 local time (UTC +3), as representative of the location of the group.

2.5 | Area used during daytime

We defined "daytime" as the time of the day during which the group traveled on average more than 50 m per hour. As such, a preliminary look at the distributions of distances covered by collared individuals per hour shows that daytime occurred, not surprisingly, between 07:00 and 19:00. Although sleeping sites were identified starting from 18:00, the group was still covering on average more than 50 m at 19:00 on 36% of all days (N = 273 days). For each day, the coordinates of the collared female from 07:00 to 19:00 were averaged, which gave a single pair of coordinates for the day. This pair of coordinates was then considered as the point in space that best represents the location the group used most during the day (henceforth center of the area used in daytime). This procedure was done for each of the 362 days of the 2014 study period and the 397 days of the 2016 study period.

2.6 | Statistical analyses

In this study, we first focused on the use of the main sleeping site, defined here as the sleeping site where the group spent most of its nights annually. For each study period, we assessed the relationships between monthly rainfall and the group's use of their main sleeping site using cross-correlation tests (95% confidence intervals [CIs]). Each cross-correlation corresponds to a correlation between the use of the main sleeping site at a given time and the amount of rainfall that occurred in each past month, with lag 0 corresponding to the amount of rainfall that occurred within the same month, lag −1 corresponding to the previous month, and so on up to lag −8, corresponding to the total amount of rainfall that occurred 8 months before. These tests were conducted to examine whether the group's use of their main sleeping site was influenced by particular amounts of rainfall in the previous months. Significant correlations were then entered into linear regressions with the group's use of the main sleeping site as the response variable and the lagged (past and present) monthly rainfall variable(s) as predictor(s) (up to the 8th month earlier). We chose to investigate lagged monthly rainfall as it has been suggested that baboons can show a delayed response to rainfall patterns (Alberts et al., 2005). We assessed the significance of predictors by comparing the model excluding the predictor with the model including all the other predictors (analysis of variance Type II). We then examined differences between wet and dry months in each study period, the frequency of use of the main sleeping site, the total

number of sleeping sites used, and the mean numbers of consecutive nights spent at the main sleeping site and at each of the other sleeping sites using Wilcoxon rank sum tests.

We also examined for each study period whether the area used during the day could predict the next sleeping site. To do so, we calculated the distance from the area used in daytime to both the chosen sleeping site and a randomly selected sleeping site not chosen that day. We subtracted the former distance by the latter as a measure of selectivity to assess whether the group selected the nearest sleeping site to where they had been most of the day. This process was iterated with a randomization test until the mean value of selectivity was stabilized (i.e., 500 times), and we examined whether the 95% CIs of the mean selectivity overlapped or not with zero.

Finally, for the 2016 study period, we used a generalized linear mixed model to assess whether or not the group chose more often the closest sleeping site in wet months or dry months. The model was fitted with a binomial error structure with the response variable being the proximity of sleeping sites (1 = baboons chose the closest sleeping site and 0 = baboons did not choose the closest sleeping site), and the predictor being wet months [1] or dry months [0]. Months (from January to December and January of the following year) were included as random effects. We only developed a generalized linear mixed model for the 2016 study period because there were only dry months in the 2014 study period (see Section 3).

All statistical analyses were conducted in R (version 3.6.3) with the following packages: "dplyr" for data manipulation (Wickham et al., 2018), "stats" for the cross-correlations (R Core Team, 2020), "lme4" for the generalized linear mixed model (Bates et al., 2007), "car" for analyses of variance (Fox & Weisberg, 2019), and ggplot2 for building figures (Wickham, 2009).

3 | RESULTS

3.1 | Rainfall in 2014 and 2016

Annual rainfall for the 2014 study period was 410.3 mm. Monthly mean temperature was 19.6°C ± SD 0.5 (range: 18.8–20.4). As monthly rainfall was relatively consistent across months, wet and dry seasons were not differentiated (Figure 1a). Based on our dichotomization of wet and dry months, with dry months having rainfall of less than 100 mm, all months during this study period were considered dry. Rainfall seasonality in 2016 was more pronounced than that in 2014 (Figure 1b), with an annual rainfall of 707.6 mm. Monthly mean temperature was 20.4°C ± SD 1.0 (range: 19.2–22.8). Wet months included January (110.2 mm), April (125.1 mm), and May (206.5 mm).

3.2 | Annual, seasonal, and monthly sleeping site use

The AI group used six sleeping sites across both study periods (Figure 2). One sleeping site (BC) consisted of a rocky cliff with
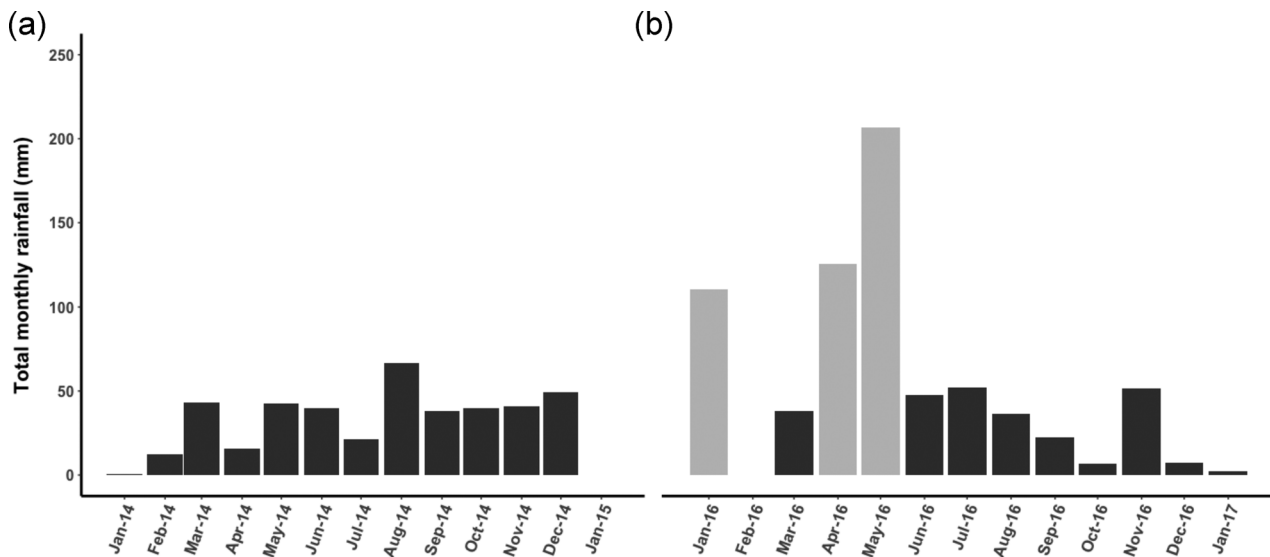
FIGURE 1 Total monthly rainfall (mm) in (a) 2014 and (b) 2016. Wet and dry months are designated by bars in gray and black, respectively

two small seasonal ponds, one on top of the cliff and one at the bottom. Field observations indicate the upper pond never dried up in 2014. Although its condition in 2016 is unknown, we expect it would have continued to hold water since 2016 was wetter than 2014. We do not have data on the lower pond as it was dangerous to approach on foot. The cliff is about 300 m long and about 22.5–38 m high from the top to the base (Matsumoto-Oda, 2015). The other sleeping sites consisted of tall *A. xanthophloea* trees (JH and MC, riverine sleeping sites) along the Ewaso Nyiro River, which flows year-round and from which the group sometimes drinks, two other rocky cliffs (MK and SE), and one rocky cliff (SF) with a seasonal waterfall. The main sleeping site of the group was BC in both periods, where it spent 83.4% of its nights (302 nights) and 46% of its nights (183 nights, Figure 3) in 2014 and 2016, respectively. The sleeping site JH was also used heavily and was the second most used sleeping site in 2016 (Figure 3b). While the two riverine sleeping sites were within approximately 2–3 km of BC, the three rocky cliff sites were 8.5–11 km away from BC.

In 2014, the group spent most of its nights at BC (Table 1). In 2016, the group spent on average a similar number of nights at BC during wet months (46.7%) and during dry months (45.6%, Table 1). Monthly rainfall during the 2014 study period was not correlated with the use of BC at any given time lag (all correlations below the CIs). In contrast to 2014, rainfall showed a significant positive cross-correlation at lag −2 with the use of BC in 2016 (penultimate month, $r = .63$). Monthly rainfall at lag −2 positively predicted the use of BC (linear regression: $\beta = 22.91$, $F_{1,9} = 12.78$, $p < .01$, adjusted $R^2 = .54$). Thus, the group's use of their main sleeping site in 2016 was predicted by the amount of rainfall two months earlier. Specifically, as rainfall increased in April and further in May, the group also increased its time there,

spending 3% and 58% of their nights, respectively, at BC (Figure 3).

In 2014, the group spent on average 15.4 ± SD 11.3 consecutive nights at BC during all months (range: 1–31 nights, Table 1). The group spent on average 1.9 ± SD 1.8 consecutive nights (range: 1–13 nights) at the four other sleeping sites. During the wet months in 2016, the group stayed at BC on average 2.5 ± SD 1.5 consecutive nights (range: 1–9 nights), and during the dry months it stayed there on average 3.6 ± SD 2.9 consecutive nights (range: 1–13 nights). This difference was not statistically significant (Wilcoxon rank sum test: $W = 18$, $p = .67$, $N = 13$). During wet months in 2016, the group stayed 6.7 consecutive nights on average ± SD 7.2 (range: 1–29 nights) at each of four sleeping sites (including BC), and during dry months, 3.5 consecutive nights on average ± SD 1.2 (range: 1–15 nights) at each of five sleeping sites (including BC). Although there was a tendency of staying more consecutive nights in each sleeping site during wet months, it was not significantly different from their use in dry months (Wilcoxon rank sum test: $W = 16$, $p = .93$, $N = 13$). Overall, the group used a similar number of sleeping sites (5) in both study periods and there was a nonsignificant trend to spend on average more consecutive nights at each sleeping site in 2014 (11 ± SD 10.2 nights) than in 2016 (4.3 ± SD 3.4 nights, Wilcoxon rank sum test: $W = 47.5$, $p = .06$, $N = 26$).

3.3 | Sleeping sites relative to area used during the day

The average distance from the center of the area used in daytime to the sleeping site chosen for the night was 1412 m ± SD 1139 in 2014 and 1145 m ± SD 889 in 2016. Overall, the mean distance between
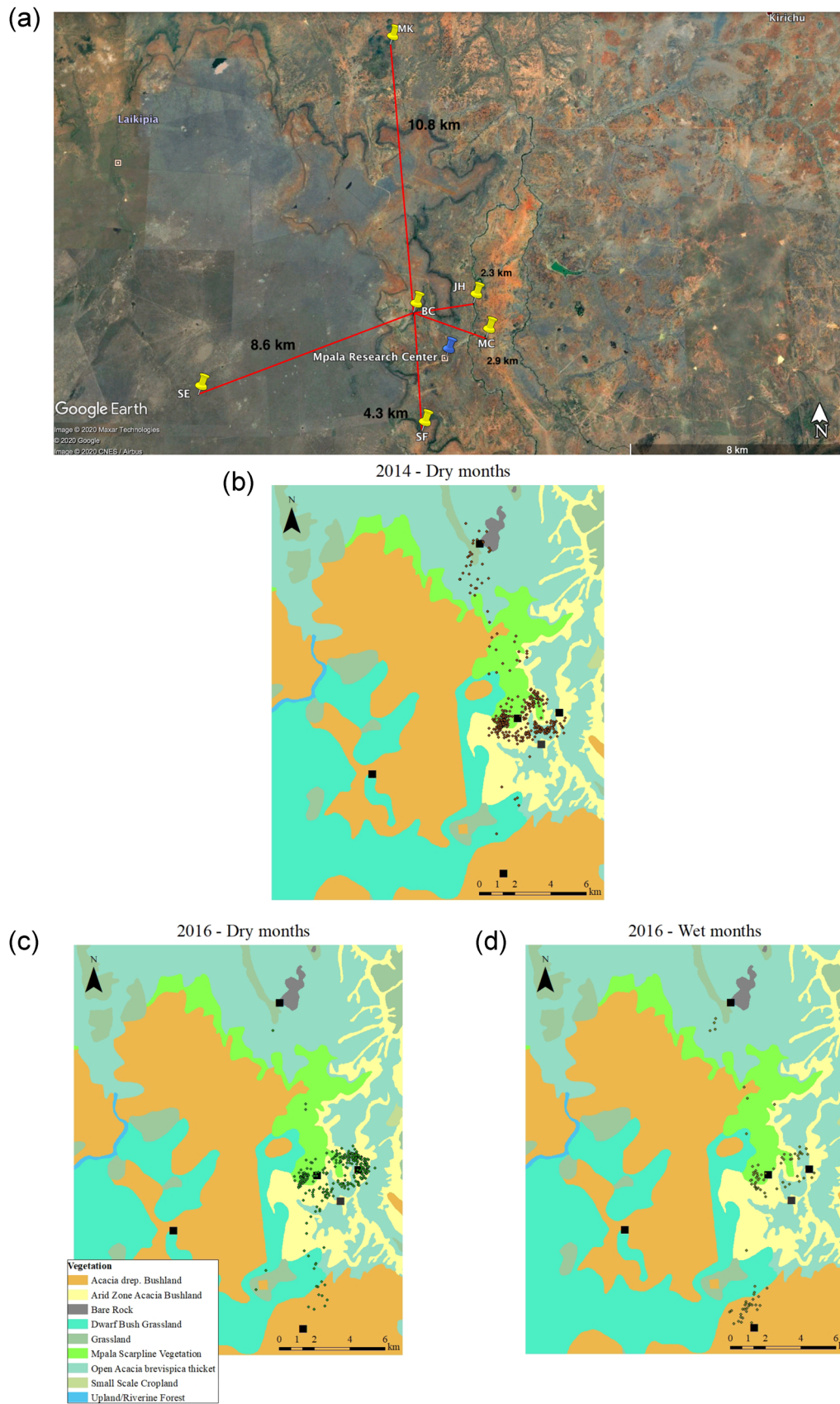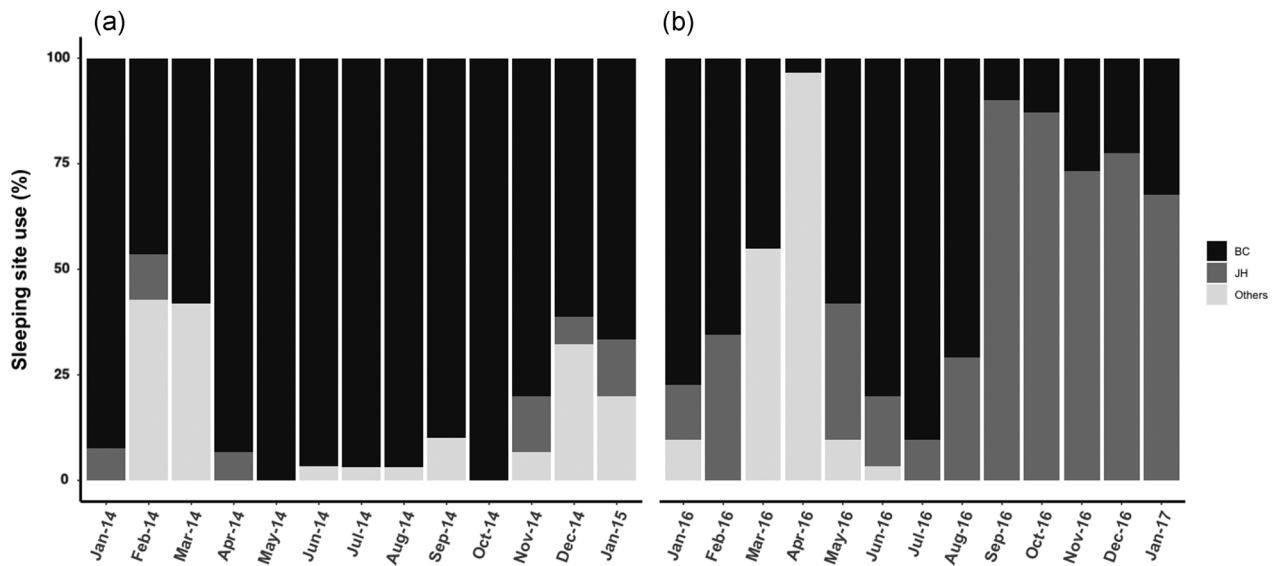
FIGURE 2 (See caption on next page)

FIGURE 3 Monthly proportion of use of sleeping sites BC and JH in (a) 2014 and (b) 2016. "Others" refers to sleeping sites MC, MK, SF, and SE combined

	2014				2016			
	Wet months (0 days)		**Dry months (362 days)**		**Wet months (92 days)**		**Dry months (305 days)**	
BC	0%	0	83.4%	15.4 (1–31)	46.7%	2.5 (1–9)	45.6%	3.6 (1–13)
JH	0%	0	3.9%	1.6 (1–3)	15%	1.3 (1–2)	48.5%	3.9 (1–15)
MC	0%	0	0.8%	1 (1–1)	0%	0	0%	0
MK	0%	0	11%	3.6 (1–13)	6.5%	3 (3–3)	0.6%	2 (2–2)
SF	0%	0	0.8%	1.5 (1–2)	31.5%	29 (29–29)	4.9%	2.2 (1–10)
SE	0%	0	0%	0	0%	0	0.3%	1 (1–1)

TABLE 1 Frequency of use of each sleeping site and mean (range) number of consecutive nights spent at each sleeping site during the wet (at least 100 mm of rain) and dry months in both study periods

Note: In 2014, there were no wet months. In 2016, wet months included January, April, and May.

the center of the area used during daytime to the chosen sleeping site was not significantly different from the distance between the center of the area used during daytime to a random sleeping site in 2014 ($p < .5$, 90% CIs did not overlap with zero) but was significantly shorter to the chosen sleeping site in 2016 ($p < .05$, 95% CIs did not overlap with zero). The percentage of nights when the group chose the closer sleeping site versus a more distant sleeping site after daytime was significantly lower in 2014 (71%) than in 2016 (83%, Wilcoxon rank sum test, $W = 45.5$, $p < .05$, $N = 23$). In 2016, there was a marginal tendency for the group to select the closer sleeping site more often during wet months than during dry months (Generalized linear mixed model: $z = -1.94$, $p = .052$).

4 | DISCUSSION

Choice of sleeping sites by baboon groups may be influenced by multiple factors, from intergroup dynamics to predator avoidance and parasitic infection (Hamilton, 1982; Hausfater & Meade, 1982; Markham et al., 2016), and here we add rainfall as a potential contributing factor. Rainfall is known to constrain the availability of food and water for baboons and consequently their feeding behavior in semi-arid habitats (Alberts et al., 2005; Barton et al., 1992; Barton, 1990; Hill & Dunbar, 2002). Thus, baboon groups should respond to patterns of rainfall in where they choose to range and where they choose to sleep. Although some of our

FIGURE 2 (a) Map of the study area (Google Earth Snapshot: 22 June 2020). The study site is located on the Laikipia Plateau, Kenya. Distances are calculated as straight lines from the main sleeping site BC. Latitude, longitude: BC 0.308°, 36.888°; JH 0.311°, 36.907°; MC 0.299°, 36.912°; MK 0.404°, 36.877°; SF 0.230°, 36.879°; SE 0.279°, 36.814°. Center of the area used in daytime (small dots) are depicted for 2014 in (b). In 2016, the center of the area used in daytime during dry months are depicted in (c) and for wet months in (d) (2014: wet months $N = 0$, dry months = 13; 2016: wet months $N = 3$, dry months = 10). Each sleeping site is represented by a black square symbol. The landscape's topology is indicated in colors

results may be consistent with this general expectation, most predictions were unsupported.

In 2014, monthly rainfall was consistently low, resulting in poorly differentiated rainfall seasonality, which compared with 2016, we predicted would lead to the use of multiple sleeping sites and short stays at each that would enable the group to search for and exploit food resources and water that may be less widely available than during periods of higher rainfall. This was not the case, however. Indeed, the group used a similar number of sleeping sites in 2014 and 2016 and, although nonsignificant, the group chose to stay for more consecutive nights at each sleeping site in 2014. The group used their main sleeping site on 83.4% of all nights in 2014 compared with 46% of all nights in 2016. One possible explanation is that if rainfall rarely reached a critical threshold for food resources to become widely available (Coe et al., 1976; Herrmann & Mohr, 2011; Rutherford, 1980), the group may actually have had less incentive to switch to other sleeping sites, especially if the main sleeping site provided benefits the other sleeping sites could not provide (see below). This result may be further supported by the fact that rainfall at different timelags did not correlate with the use of BC, the main sleeping site, in 2014. In 2016, rainfall seasonality was more marked but the group used their main sleeping site on only 46% of all nights, again, a finding we had not predicted. On a monthly timescale, there was a nonsignificant trend for the group to reduce the number of sleeping sites it used, and it stayed at these sites for more consecutive nights during wet months compared to dry months. This trend might be consistent with the expectation that primates require a smaller area in which to forage as food availability increases (Milton & May, 1976).

We also predicted that the group would choose to sleep at sites closer to where they spent most of their time during the day more often in wet months than in dry months. This also follows the expectation that a richer environment will allow primates to range and forage in a smaller area. We reasoned that if foods became more abundant during wet months, the group would not need to range as far to forage and would be less likely to deplete foods near their sleeping sites. This would then also be reflected in shorter daily travel distances from the area most used during the day to the nightly sleeping site. On a yearly timescale, this was supported. The group chose the closer sleeping site more often in the wetter 2016 study period than in the drier 2014 study period and its average daily travel distance from the center of the area used in daytime to that night's sleeping site was also shorter in 2016. On a monthly timescale, this prediction was less supported for 2016, although there was a tendency in wet months for the group to spend more of its nights at sleeping sites closer to the areas it had used most on those same days than in dry months.

Several limitations to the current study must be mentioned, particularly with respect to the sample size and the available data. First, mapping the location and availability of water and food resources across time and space (for instance by using the normalized difference vegetation index; Zinner, 2001) and establishing their relationship to rainfall is necessary to support the idea that rainfall directly influences sleeping site selection. Although several studies have suggested a link between rainfall, food availability, and foraging behaviors (Alberts et al., 2005; Barton, 1990; Hill & Dunbar, 2002; Naughton-Treves et al., 1998), its effect remains to be demonstrated, as previously suggested by other authors (Markham et al., 2016).

Second, our sample sizes are limited to two 13-month study periods that were extremely different in both rainfall and sleeping site use, which limits the power of our analyses. As such, analyses over longer time periods (i.e., decades, especially in East Africa where interannual rainfall is highly variable: Herrmann & Mohr, 2011) are crucial because they may reveal a clearer picture of how rainfall influences sleeping site selection. This might also partially explain why some nonsignificant tendencies were found in the predicted directions.

Third, we lack sufficient data on other factors that likely affect sleeping site selection, such as predation and parasitic avoidance to include them here. Thus, our analyses were reduced to fitting one behavior to a single variable (rainfall), which may seem overly simplistic and may also explain why some of our predictions were unsupported. For instance, preferences for the sleeping site BC may also be related to better protection or greater perceived protection from predators than other sleeping sites, as nocturnal predation by leopards (*Panthera pardus*) has been suggested to affect the use of cliffside and riverine sleeping sites in this population of baboons (Bidner et al., 2018). During the 2014 study period, a concurrent study on leopard–baboon dynamics that monitored four baboon groups, including the one described here, found that baboon groups overall preferred to sleep at cliffside sites rather than riverine sites. As leopards visited riverine sleeping sites more often than cliffside sleeping sites at night, it is possible that the baboons perceived a lower risk of leopard predation at BC and other cliffside sites (even though baboons are killed at both types of sites, Bidner et al., 2018; Isbell et al., 2018; Matsumoto-Oda, 2015). However, this would not explain why the AI group preferred BC over other cliffside sites. In fact, each baboon group in this population has one primary sleeping site and these are rarely shared with other groups (Bidner et al., 2018). Thus, a third factor influencing sleeping site selection may be intergroup interactions, in that having a primary sleeping site may reduce the potential for intergroup conflict.

Finally, one largely understudied factor influencing sleeping site selection is the effect of parasites. Groups may frequently switch sleeping sites as fecal matter accumulates there to reduce parasitic infection, depending on the lifecycles of parasites (Hausfater & Meade, 1982). Overall, investigating the interrelationships of all above-mentioned factors (including rainfall) is thus necessary to fully understand sleeping site selection. Nonetheless, we suggest that rainfall can be a potentially important factor to consider, particularly in areas of Africa with highly variable interannual rainfall, and is an interesting avenue for further research.

AUTHOR CONTRIBUTIONS

Alexandre Suire: conceptualization; formal analysis; visualization; writing original draft; writing review & editing. **Lynne A. Isbell**: funding acquisition; investigation; writing review & editing. **Laura R. Bidner**: funding acquisition; investigation; writing review & editing. **Yushin Shinoda**: formal analysis; visualization; writing review & editing. **Munemitsu Akasaka**: formal analysis; writing review & editing. **Akiko Matsumoto-Oda**: conceptualization; funding acquisition; investigation; supervision; writing review & editing.

DATA AVAILABILITY STATEMENT

GPS data for 2014–2015 are deposited in the Movebank data repository (https://www.movebank.org) and are available upon reasonable request to LAI. GPS data for 2016–2017 are available upon request to AMO.

ORCID

Alexandre Suire https://orcid.org/0000-0002-1852-3083
Lynne A. Isbell https://orcid.org/0000-0002-2285-6411
Laura R. Bidner https://orcid.org/0000-0002-4198-6609
Yushin Shinoda https://orcid.org/0000-0002-1605-6303
Munemitsu Akasaka https://orcid.org/0000-0002-0143-0841
Akiko Matsumoto-Oda https://orcid.org/0000-0002-8076-5534

REFERENCES

Alberts, S. C., & Altmann, J. (2006). The evolutionary past and the research future: Environmental variation and life history flexibility in a primate lineage. In L. Swell, & S. R. Leigh (Eds.), *Reproduction and fitness in baboons: Behavioral, ecological, and life history perspectives* (pp. 277–303). Springer.

Alberts, S. C., Hollister-Smith, J., Mututua, R. S., Sayialel, S. N., Muruthi, P. M., Warutere, J. K., & Altmann, J. (2005). Seasonality and long term change in a savannah environment. In D. K. Brockman, & C. P. Schaik (Eds.), *Seasonality in primates: Studies of living and extinct human and nonhuman primates* (pp. 157–196). Cambridge University Press.

Altmann, S. A., & Altmann, J. (1970). *Baboon ecology: African field research.* University of Chicago Press.

Barrett, L. (2009). A guide to practical babooning: Historical, social, and cognitive contingency. *Evolutionary Anthropology: Issues, News, and Reviews*, 18(3), 91–102. https://doi.org/10.1002/evan.20210

Barton, R. A. (1990). *Foraging strategies, diet and competition in olive baboons* (Unpublished doctoral dissertation). University of St Andrews.

Barton, R. A., Byrne, R. W., & Whiten, A. (1996). Ecology, feeding competition and social structure in baboons. *Behavioral Ecology and Sociobiology*, 38(5), 321–329. https://doi.org/10.1007/s002650050248

Barton, R. A., Whiten, A., Strum, S. C., Byrne, R. W., & Simpson, A. J. (1992). Habitat use and resource availability in baboons. *Animal Behaviour*, 43(5), 831–844. https://doi.org/10.1016/S0003-3472(05)80206-4

Bates, D., Sarkar, D., Bates, M. D., & Matrix, L. (2007). The lme4 package. *R package version*, 2(1), 74.

Bidner, L. R., Matsumoto-Oda, A., & Isbell, L. A. (2018). The role of sleeping sites in the predator-prey dynamics of leopards and olive baboons. *American Journal of Primatology*, 80(12), e22932. https://doi.org/10.1002/ajp.22932

Chapman, C. (1988). Patterns of foraging and range use by three species of neotropical primates. *Primates*, 29(2), 177–194. https://doi.org/10.1007/BF02381121

Chapman, C. A. (1989). Spider monkey sleeping sites: Use and availability. *American Journal of Primatology*, 18(1), 53–60. https://doi.org/10.1002/ajp.1350180106

Coe, M. J., Cumming, D. H., & Phillipson, J. (1976). Biomass and production of large African herbivores in relation to rainfall and primary production. *Oecologia*, 22(4), 341–354. https://doi.org/10.1007/BF00345312

Fox, J., & Weisberg, S. (2019). *An R companion to applied regression (3rd edition).* Sage.

Gursky, S. (2000). Effect of seasonality on the behavior of an insectivorous primate, *Tarsius spectrum. International Journal of Primatology*, 21(3), 477–495. https://doi.org/10.1023/A:1005444020059

Hamilton, W. J. (1982). Baboon sleeping site preferences and relationships to primate grouping patterns. *American Journal of Primatology*, 3(1-4), 41–53. https://doi.org/10.1002/ajp.1350030104

Hausfater, G., & Meade, B. J. (1982). Alternation of sleeping groves by yellow vaboons (*Papio cynocephalus*) as a strategy for parasite avoidance. *Primates*, 23(2), 287–297. https://doi.org/10.1007/BF02381167

Herrmann, S. M., & Mohr, K. I. (2011). A continental-scale classification of rainfall seasonality regimes in Africa based on gridded precipitation and land surface temperature products. *Journal of Applied Meteorology and Climatology*, 50(12), 2504–2513. https://doi.org/10.1175/JAMC-D-11-024.1

Hill, R. A., & Dunbar, R. I. M. (2002). Climatic determinants of diet and foraging behaviour in baboons. *Evolutionary Ecology*, 16(6), 579–593. https://doi.org/10.1023/A:1021625003597

Holmes, T. D., Bergstrom, M. L., & Fedigan, L. M. (2011). Sleeping site selection by white-faced capuchins (*Cebus capucinus*) in the Area de Conservación Guanacaste, Costa Rica. *Ecological and Environmental Anthropology*, 6, 9.

Isbell, L. A., Bidner, L. R., Omondi, G., Mutinda, M., & Matsumoto-Oda, A. (2019). Capture, immobilization, and Global Positioning System collaring of olive baboons (*Papio anubis*) and vervets (*Chlorocebus pygerythrus*): Lessons learned and suggested best practices. *American Journal of Primatology*, e22997. https://doi.org/10.1002/ajp.22997

Isbell, L. A., Bidner, L. R., Van Cleave, E. K., Matsumoto-Oda, A., & Crofoot, M. C. (2018). GPS-identified vulnerabilities of savannah-woodland primates to leopard predation and their implications for early hominins. *Journal of Human Evolution*, 118, 1–13. https://doi.org/10.1016/j.jhevol.2018.02.003

Malenky, R. K., & Wrangham, R. W. (1994). A quantitative comparison of terrestrial herbaceous food consumption by *Pan paniscus* in the Lomako Forest, Zaire, and *Pan troglodytes* in the Kibale Forest, Uganda. *American Journal of Primatology*, 32(1), 1–12. https://doi.org/10.1002/ajp.1350320102

Markham, A. C., Alberts, S. C., & Altmann, J. (2016). Haven for the night: Sleeping site selection in a wild primate. *Behavioral Ecology*, 27(1), 29–35. https://doi.org/10.1093/beheco/arv118

Markham, A. C., Guttal, V., Alberts, S. C., & Altmann, J. (2013). When good neighbors don't need fences: Temporal landscape partitioning among baboon social groups. *Behavioral Ecology and Sociobiology*, 67(6), 875–884. https://doi.org/10.1007/s00265-013-1510-0

Matsumoto-Oda, A. (2015). How surviving baboons behaved after leopard predation: A case report. *Anthropological Science*, 123(1), 13–17. https://doi.org/10.1537/ase.150223

Matsumoto-Oda, A., & Palombit, R. A. (2015). Activity budgets and rainfall seasonality in a wild baboon (*Papio anubis*) group. *Primate Research*, 31, 013–107. https://doi.org/10.2354/psj.31.013

Milton, K., & May, M. L. (1976). Body weight, diet and home range area in primates. *Nature*, 259(5543), 459–462. https://doi.org/10.1038/259459a0

Naughton-Treves, L., Treves, A., Chapman, C., & Wrangham, R. (1998). Temporal patterns of crop-raiding by primates: Linking food availability in croplands and adjacent forest. *Journal of Applied Ecology*, 35(4), 596–606. https://doi.org/10.1046/j.1365-2664.1998.3540596.x

Overdorff, D. J. (1996). Ecological correlates to activity and habitat use of two prosimian primates: *Eulemur rubriventer* and *Eulemur fulvus rufus* in Madagascar. *American Journal of Primatology*, 40(4), 327–342. https://doi.org/10.1002/(SICI)1098-2345(1996)40:4<327::AID-AJP3>3.0.CO;2-%23

Palombit, R. A. (2013). *Papio anubis* olive baboon. In T. M. Butynski, & J. Kingdon (Eds.), *The mammals of Africa: Vol II primates* (pp. 233–239). Bloomsbury Publishing.

Pontes, A. R. M., & Soares, M. L. (2005). Sleeping sites of common marmosets (*Callithrix jacchus*) in defaunated urban forest fragments: A strategy to maximize food intake. *Journal of Zoology*, 266(1), 55–63. https://doi.org/10.1017/S095283690500662X

Post, D. G. (1981). Activity patterns of yellow baboons (*Papio cynocephalus*) in the Amboseli National Park, Kenya. *Animal Behaviour*, 29(2), 357–374. https://doi.org/10.1016/S0003-3472(81)80095-4

R Core Team. (2020). *R: A language and environment for statistical computing.* https://www.R-project.org/

Rubenstein, D. R. (2011). Spatiotemporal environmental variation, risk aversion, and the evolution of cooperative breeding as a bet-hedging strategy. *Proceedings of the National Academy of Sciences of the United States of America*, 108(2), 10816–10822. https://doi.org/10.1073/pnas.1100303108

Rutherford, M. C. (1980). Annual plant production-precipitation relations in arid and semi-arid regions. *South African Journal of Science*, 76(2), 53–57.

Scholz, F., & Kappeler, P. M. (2004). Effects of seasonal water scarcity on the ranging behavior of *Eulemur fulvus rufus*. *International Journal of Primatology*, 25(3), 599–613. https://doi.org/10.1023/B:IJOP.0000023577.32587.0b

Schreier, A. L. (2009). *The influence of resource distribution on the social structure and travel patterns of wild hamadryas baboons (Papio hamadryas) in Filoha, Awash National Park, Ethiopia* (Unpublished doctoral dissertation). City University of New York, NY.

Sikes, R. S., The Animal Care and Use Committee of the American Society of Mammalogists. (2016). 2016 Guidelines of the American Society of Mammalogists for the use of wild mammals in research and education. *Journal of Mammalogy*, 97(3), 663–688. https://doi.org/10.1093/jmammal/gyw078

Strier, K. B. (1991). Diet in one group of woolly spider monkeys, or muriquis (*Brachyteles arachnoides*). *American Journal of Primatology*, 23(2), 113–126. https://doi.org/10.1002/ajp.1350230205

Teichroeb, J. A., Holmes, T. D., & Sicotte, P. (2012). Use of sleeping trees by ursine colobus monkeys (*Colobus vellerosus*) demonstrates the importance of nearby food. *Primates*, 53(3), 287–296. https://doi.org/10.1007/s10329-012-0299-1

Von Hippel, F. A. (1998). Use of sleeping trees by black and white Colobus monkeys (*Colobus guereza*) in the Kakamega Forest, Kenya. *American Journal of Primatology*, 45(3), 281–290. https://doi.org/10.1002/(SICI)1098-2345(1998)45:3<281::AID-AJP4>3.0.CO;2-S

Walter, H., & Lieth, H. (1960). *Klimadiagramm-Weltatlas (Climate Diagram World Atlas)*. Fischer-Verlag.

Wang, S., Luo, Y., & Cui, G. (2011). Sleeping site selection of Francois's langur (*Trachypithecus francoisi*) in two habitats in Mayanghe National Nature Reserve, Guizhou, China. *Primates*, 52(1), 51–60. https://doi.org/10.1007/s10329-010-0218-2

Whiten, A., Byrne, R. W., Barton, R. A., Waterman, P. G., Henzi, S. P., Hawkes, K., Widdowson, E. M., Altmann, S. A., Milton, K., & Dunbar, R. I. M. (1991). Dietary and foraging strategies of baboons. *Philosophical Transactions: Biological Sciences*, 334(1270), 187–197. http://www.jstor.org/stable/55456

Wickham, H. (2009). *Ggplot2: Elegant graphics for data analysis.* Springer.

Wickham, H., François, R., Henry, L., & Müller, K. (2018). *Dplyr: A grammar of data manipulation. R package version 0.7.8.* https://CRAN.R-project.org/package=dplyr

Wrangham, R. W., Conklin-Brittain, N. L., & Hunt, K. D. (1998). Dietary response of chimpanzees and cercopithecines to seasonal variation in fruit abundance. I. Antifeedants. *International Journal of Primatology*, 19(6), 949–970. https://doi.org/10.1023/A:1020318102257

Zinner, D. (2001). Distribution and habitat associations of baboons (*Papio hamadryas*) in Central Eritrea. *International Journal of Primatology*, 22, 17–413. https://doi.org/10.1023/A:1010703611820