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## Original Article

# Haven for the night: sleeping site selection in a wild primate

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Many animals seek refuge when they sleep, often employing different sleeping sites in successive time periods. Switching from one sleeping site to another might reduce predation or parasite exposure or increase proximity to food resources that are temporally and spatially heterogeneous. However, achieving these effects will depend on the synchronous and nonsynchronous use of the same sleeping sites by conspecifics. We assessed the use of multiple sleeping sites by 5 wild baboon (*Papio cynocephalus*) social groups to evaluate how sites were exploited at both the population and group level. Of 126 woodland sleeping sites used by the study population over ~900 nights of observation, 10 sites were used more than 100 times; these preferred sites accounted for ~60% of all known sleeping sites. On average, individual groups left sleeping sites after 1–2 nights of continuous use, and the same group did not reuse a site for an average of 45 nights. However, at the population level, preferred sites were reused on average every 4 nights. This near-continuous occupation suggests that groups competed for access to preferred sites, perhaps because preferred sites represented better protection from predators, lower parasite prevalence, or had better foraging opportunities nearby. The number of trees in a sleeping site and the time since a site was last used were significant factors distinguishing sites used on a given night by the most dominant versus most subordinate social group. These findings highlight the importance of evaluating resource use at multiple levels of social organization.

**Key words:** multiple central place forager, *Papio cynocephalus*, parasite, predation, sleep, wild baboons.

## INTRODUCTION

Animals in a wide range of taxa vary their use of sleeping sites rather than consistently using a single site for long periods. This tendency to switch sleeping sites has been documented in bats (reviewed in Lewis 1995), birds (e.g. Morrison and Caccamise 1985; Stouffer and Caccamise 1991), burrowing mammals (Roper et al. 2001, 2002), and primates (reviewed in Anderson 1998). The use of multiple sleeping sites is presumed to reflect the fact that sleeping site quality declines as a function of nights of consecutive occupancy because continuous occupancy could increase the risk of predation (Bert 1973; Hrdy 1977; Heymann 1995), increase the probability of parasitic infection (Hausfater and Meade 1982; Butler and Roper 1996; Reckardt and Kerth 2007), and/or reduce opportunities to monitor and exploit locally available foraging resources (Chapman 1989; von Hippel 1998; Lewis 1996). If any of these relationships occurred, then optimal patterns of sleeping site reuse would depend on time-dependent

changes in predator memory, parasite life cycles, and/or renewal of foraging resources. Measuring the duration of continuous sleeping site occupancy, and intervals since a site was last used, is thus important for shedding light on possible explanations for the use of multiple sleeping sites.

For nonterritorial species, in which neighbors share access to sleeping sites in regions of home range overlap, optimal patterns of sleeping site use will depend not only on an individual's (or social group's) own use of a site but also the site's use by conspecifics. However, studies rarely have addressed how sharing of sleeping sites among conspecifics—both synchronously and nonsynchronously—influences the temporal pattern of sleeping site occupancy (but see Day and Elwood 1999). As such, how overall population patterns of site use compare with the patterns exhibited by individuals are poorly understood. In addition, whether resource use by conspecifics differentially influences when dominant versus subordinate individuals (or groups) access shared sites has been unknown.

Here, we capitalize on an opportunity to quantify sleeping site use and time intervals until site reuse in social groups of wild baboons (*Papio cynocephalus*). Baboons, like many other

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cercopithecine primates, live in discrete and stable multimale–multifemale social groups (Altmann SA and Altmann J 1970; Estes 1991). Multiple social groups make up a single population, and the home ranges of neighboring baboon groups overlap extensively (e.g., Altmann SA and Altmann J 1970; Shopland 1982; Markham et al. 2013). Limited resources, including sleeping sites, are usually located within regions of overlap (Altmann SA and Altmann J 1970). Here, we assessed 1) patterns of sleeping site use by individual social groups and by the whole study population, 2) the ecological attributes that predicted frequency of use among sleeping sites, and 3) factors influencing site use for the most dominant social group in the study population relative to the most subordinate social group. Together, these analyses provide novel insight into the consequences of resource sharing. Evaluating the hypothesis that priority of access to preferred resources is one benefit of social dominance, we predicted that the most dominant social group in the population should preferentially have access to the highest quality sleeping sites.

## METHODS

### Study subjects and GPS collars

The study subjects were wild baboons living in the Amboseli basin of East Africa, a semi-arid short-grass savannah with interspersed woodlands of *Acacia xanthophloea* and *Acacia tortilis* (Alberts et al. 2005; Croze and Lindsay 2011). This baboon population has been the subject of continuous observation since 1971 through the Amboseli Baboon Research Project (ABRP). Complete details on ABRP monitoring effort and data collection protocols can be accessed online (<https://amboselibaboons.nd.edu/>, last accessed 24 June 2015).

From 1 April 2008 to 31 August 2010, we used GPS collars (model G2110B, Advanced Telemetry Systems Inc., Isanti, MN) to synchronously monitor the movements of the 5 social groups that are part of a single study population. Specifically, we collared a single individual at a time within each study group. Each collar was equipped with an automated drop-off mechanism and was pre-programmed to release after 300 days, a time duration based on manufacturer calculations for expected battery life and ABRP field testing of equipment (Markham and Altmann 2008). We preferentially collared adult females because females remain in their natal groups throughout their lives, eliminating the risk of dispersal. Males were collared in only 2 instances when there were no suitable female candidates at the time of collar deployment (i.e., all adult females in a given group were pregnant or had dependent young). We programmed each individual's collar to record hourly locations during the portion of the day that baboons are active (0600–1900). Baboons are usually asleep between 1900 and 0600h the following morning, and spatial displacement is minimal during these hours. Using GPS collar data from 5649 paired 1900 and 0600h readings, we found that baboons moved  $16.8 \pm 0.61$  m (mean  $\pm$  standard error [SE]) between 1900 and 0600h the following morning. Full details on GPS collar deployment and monitoring effort are provided in Markham et al. (2013).

### Sleeping sites

We determined sleep location for 4270 group-nights. We used the 1900h location as indicative of the group's sleep location if this location fell within the perimeter of a woodland area. Baboons in the Amboseli region only use woodland areas as sleeping sites (Altmann SA and Altmann J 1970). Cliffs and rocky outcroppings,

which are used as sleeping sites by baboons in some other populations (Hamilton 1982), are not present within the range of the ABRP study population. If the 1900 reading was missed by the GPS collar ( $N = 72$ ) or if the 1900 reading was not under canopy cover ( $N = 352$ ), we used the next morning's 0600 reading as representative of the night's sleeping site if the 0600 reading was within the perimeter of a woodland; otherwise, we considered that we had missed the sleeping site ( $N = 44$ ). Sleeping locations on an additional 99 nights were missed due to gaps in monitoring between successive rounds of GPS collar deployment in a given group (median gap length 7 days;  $N = 7$  gaps).

Per long-standing ABRP field protocols, we defined a grove as a woodland area in which the baboons could move from one tree to a neighboring tree without descending to the ground. To delineate the boundaries of each grove, we walked the outermost canopy edge of a given grove while recording our travel path using a handheld GPS unit. This path was later plotted as the grove perimeter in Esri ArcGIS 9.2 (Environmental Systems Resources Institute, Inc., Redlands, CA). To account for marginal errors in the accuracy of GPS data from the collars and handheld units used for mapping, any set of groves that had canopies within 20 m of each other were considered to be a single sleeping site. Groves were clustered together as sleeping sites using Esri ArcGIS.

### Sleeping site occupancy

We assessed duration of continuous occupancy of each sleeping site and the time until reuse at both the population and group levels. For the population-level assessments we combined data on site use from all 5 study groups. Only sites used more than once at the population level were included in analyses. We calculated duration of continuous occupancy by counting the total number of nights that a site was used without interruption. We considered each set of successive nights of site occupancy to be “bouts of continuous occupancy.” We calculated time until reuse as the interval between the first night a site was left unused and the night of its next occupancy (or, for censored intervals, the last night on which sleeping sites of all 5 social groups were known: see below for details). We considered each set of successive nights that a site was not occupied as “intervals of vacancy.” We used Kaplan–Meier survival analysis with Mantel Cox log rank test to compare population versus group-level patterns of duration of 1) bouts of continuous occupancy and 2) intervals of vacancy. Occasionally, we were unable to definitively locate the sleeping site of one or more of the 5 groups on a given night because of ambiguous or missing GPS readings (see above). This resulted in some bouts of occupancy and vacancy being censored. For population-level patterns, bouts of continuous occupancy were coded as censored (16.1% of 3001 bouts) if the sleeping sites of any of the 5 social groups were unknown on the night either immediately preceding or following a night of confirmed site occupancy. Intervals of vacancy at the population level were coded as censored (38.0% of 2999 intervals) if 1) the site was not reused before the study's end or 2) the sleeping sites of any of the 5 social groups were unknown on a night in the interval between the site's last confirmed and subsequent use. For group-level patterns, bouts of continuous occupancy were coded as censored (3.0% of 3409 bouts) if the sleeping site of the focal group was unknown on either the day immediately preceding or following occupancy. Intervals of vacancy at the group level were coded as censored (5.6% of 3405 intervals) if 1) the site was not reused before the study's end or 2) the sleeping site of the focal group was unknown on a night in the interval between the site's last confirmed and subsequent use.

## Predicting sleeping site use

We assessed several attributes that were possible predictors of how frequently a sleeping site was used: 1) the dominant tree species in the sleeping site (*A. xanthophloea* or *A. tortilis*); 2) number of trees in the sleeping site; 3) health of each tree in a sleeping site; 4) maximum canopy height for each tree in a sleeping site; and 5) diameter at breast height (DBH) of each tree in a sleeping site. We quantified tree health on a 4-point scale: “4”: healthiest, >75% branches alive; “3”: 75–50% branches alive; “2”: 25–50% branches alive; “1”: severely moribund, <25% branches alive. We computed values for health, maximum canopy height, and DBH for each sleeping site as the average value for each measure using data on each individual tree within the site. We entered these values, along with tree species and number of trees in the sleeping site, as the independent variables in a generalized linear model with negative binomial errors to predict the number of times each sleeping site was used. Sleeping site use was calculated as the number of times a sleeping location fell within the perimeter of any of the individual groves comprising the sleeping site.

Distances separating sleeping sites on consecutive nights and daily travel distances were calculated in Esri ArcGIS. Daily travel distance assumed straight-line movement between consecutive hourly locations. We used a generalized estimating equation (GEE) controlling for repeated measures of the same group to test the factors predicting whether a group reused the site it had slept in the previous night. Predictor variables included 1) daily distance traveled by the group and 2) whether a sleeping site was preferred or nonpreferred (see Results for distinction of preferred vs. nonpreferred sites).

Finally, we used a GEE to test the factors predicting sleeping site use by the most dominant group in the population relative to the most subordinate group. We used the number of adult males in each group to assess group-level dominance because this is a strong predictor of one group's ability to displace another (Markham et al. 2012). This analysis included only nights on which the sleeping sites for both of these groups were known ( $N = 764$  nights); date of observation was entered as a repeated measure in the model. Predictor variables included the number of trees comprising the sleeping site and nights since the site was last used by any of the 5 social groups in the study population.

All statistical tests were performed in SPSS 22.0 (SPSS Inc., Chicago, IL). The alpha value for significance was set to 0.05.

## Ethical note

All project protocols complied with regulations in Kenya (Republic of Kenya Research Permits NCST/5/002/R/776 to J.A. and NCST/5/002/R/777 to S.C.A.) and in the United States (Princeton University IACUC 1649) and adhered to the ASAB/ABS Guidelines for the Use of Animals in Research.

## RESULTS

Of the 126 sleeping sites used collectively by the study population between 1 April 2008 and 31 August 2010, 10 were used over 100 times each. We designated these as “preferred sites” (Figure 1). These preferred sites constituted only 7.9% of all sleeping sites but accounted for 58.9% of all records of sleeping sites ( $N = 2517$  group-nights). See Table 1 for a comparison of number of trees, tree health, maximum canopy height, and DBH at preferred versus nonpreferred sleeping sites.

## Bouts of continuous occupancy and intervals of vacancy

We differentiated bouts of continuous occupancy and intervals of vacancy at the population level (counting site use by any combination of the study groups) versus at the group level (counting site use by a single group). Bouts of continuous occupancy at the population level were significantly longer, on average, than bouts of continuous occupancy at the group level (1.7 nights  $\pm$  0.03 SE vs. 1.3 nights  $\pm$  0.01 SE;  $N = 3001$  and  $N = 3409$  bouts of continuous occupancy, respectively; Mantel Cox log rank,  $\chi^2 = 255.7$ , degrees of freedom [df] = 1,  $P < 0.001$ ). At the population level, bouts of continuous occupancy at the 10 preferred sites were significantly longer, on average, than bouts of continuous occupancy at nonpreferred sites (2.0 nights  $\pm$  0.05 SE vs. 1.4 nights  $\pm$  0.04 SE;  $N = 1459$  and  $N = 1542$  bouts of continuous occupancy, respectively; Mantel Cox log rank,  $\chi^2 = 158.6$ , df = 1,  $P < 0.001$ ; Figure 2).

Intervals of vacancy at the population level were significantly shorter, on average, than intervals of vacancy at the group level (15.1 nights  $\pm$  0.84 SE vs. 45.0 nights  $\pm$  2.6 SE,  $N = 2999$  and  $N = 3405$  intervals, respectively; Mantel Cox log rank,  $\chi^2 = 73.6$ , df = 1,  $P < 0.001$ ). At the population level, intervals of vacancy at the 10 preferred sites were significantly shorter, on average, than intervals of vacancy at nonpreferred sites (4.1 nights  $\pm$  0.21 SE vs. 25.8 nights  $\pm$  1.54 SE;  $N = 1428$  and  $N = 1541$ , respectively; Mantel Cox log rank,  $\chi^2 = 830.0$ , df = 1,  $P < 0.001$ ; Figure 3).

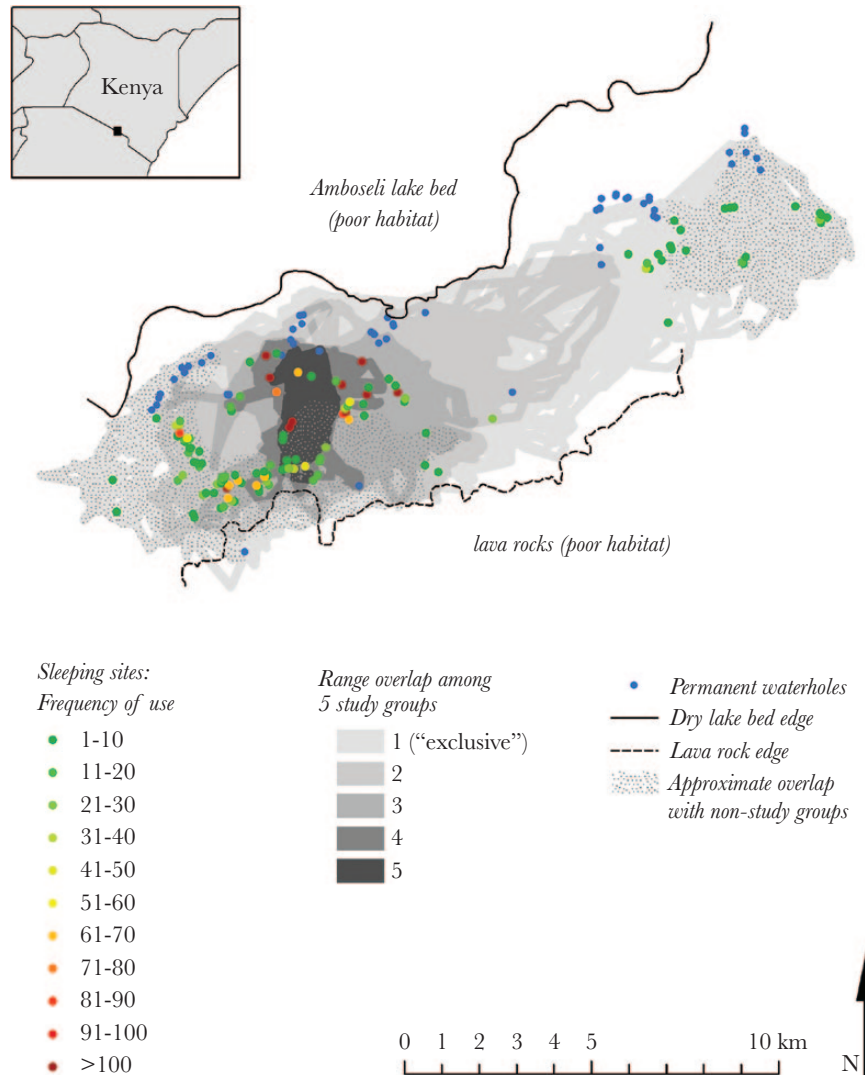
To minimize exposure to fecal parasites, Hausfater and Meade (1982) posited that the optimal interval of continuous sleeping site use for baboon groups was 2 nights at most and that the optimal interval of vacancy was more than 8.5 nights (see Discussion). We found that 83.5% of all occupancy bouts were indeed 1 or 2 nights at the preferred sites, and this value increased to 98.2% of bouts for nonpreferred sleeping sites. However, we found that only 9.5% of intervals of vacancy were >8.5 nights at preferred sites although this value increased to 54.1% of intervals for nonpreferred sites. Compared with these population-level patterns of sleeping site use, 95.3% ( $\pm$  0.92 SE) of occupancy bouts by a single group were 1 or 2 nights and 40.4% ( $\pm$  2.05 SE) of intervals of vacancy at the group level were >8.5 nights.

## Distances separating sleeping sites on consecutive nights and daily travel distance

On 66.3% of nights, a group's sleeping site was >500 m from its sleeping site on the previous night ( $N = 2801$  records). When a group's sleeping site was within 500 m of its sleeping site on the previous night, this often meant that the group was reusing the same site it had used the previous night ( $N = 862$  of 1418 records or 60.8% of cases in which the group slept within 500 m of its previous night's site). These analyses were performed on the straight-line distance between sleeping sites, regardless of the distance the baboon group traveled on a given day. Explicitly assessing how site reuse related to daily travel distance, we found that a group was more likely to return to the sleeping site it had used on the previous night when the group's daily travel distance was shorter ( $N = 4268$  group-travel days;  $B = -0.181$ , Wald  $\chi^2 = 8.6$ , df = 1,  $P = 0.003$ ) and when the sleeping site was preferred ( $B = -1.107$  for nonpreferred sites, Wald  $\chi^2 = 256.7$ , df = 1,  $P < 0.001$ ).

## Predictors of sleeping site use

Sleeping sites were used more frequently when they had a larger number of trees within the sleeping site ( $N = 124$  sleeping sites;

**Figure 1**

Distribution of sleeping sites (color coded for the number of nights they were used) and permanent waterholes, relative to the ranges of 5 baboon social groups observed from 1 April 2008–31 August 2010.

**Table 1**

**Average ( $\pm$  SE) and range of number of trees, tree health, maximum canopy height, and DBH for preferred ( $N = 10$ ) versus nonpreferred ( $N = 116$ ) sleeping sites**

	Preferred sites		Nonpreferred sites	
	Mean $\pm$ SE	Range	Mean $\pm$ SE	Range
Number of trees	8 $\pm$ 10.1	9–108	6 $\pm$ 0.4	1–22
Tree health <sup>a</sup>	3.6 $\pm$ 0.05	3.5–4.0	3.6 $\pm$ 0.03	2.6–4.0
Maximum canopy height (m)	18.0 $\pm$ 0.38	16.3–20.1	17.8 $\pm$ 0.31	8.0–26.1
DBH (cm)	64.3 $\pm$ 2.13	55.1–79.1	71.9 $\pm$ 1.62	44.0–160.5

<sup>a</sup>Tree health was assessed on a 4-point scale ranging from “1” for severely moribund to “4” for healthiest; see Methods for details.

$B = 0.106$ , Wald  $\chi^2 = 33.6$ ,  $df = 1$ ,  $P < 0.001$ ; **Supplementary Figure 1**) and when the trees in the sleeping site were more healthy ( $B = 0.840$ , Wald  $\chi^2 = 6.7$ ,  $df = 1$ ,  $P = 0.010$ ). By contrast, sleeping site use was not predicted by average maximum canopy height of trees in the sleeping site ( $B = 0.018$ , Wald  $\chi^2 = 0.2$ ,  $df = 1$ ,  $P = 0.682$ ) or average DBH of trees in the sleeping site ( $B = -0.005$ , Wald  $\chi^2 = 0.4$ ,  $df = 1$ ,  $P = 0.514$ ). Tree species

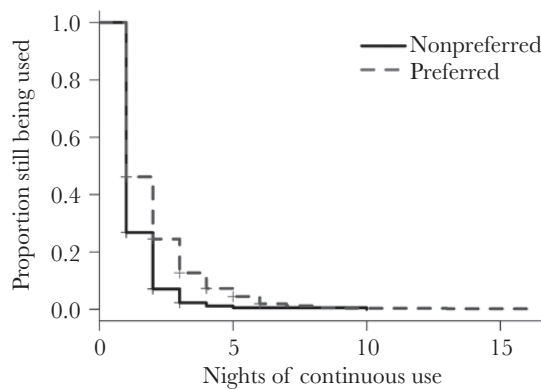
revealed a nonsignificant trend toward predicting use frequency ( $B = 0.588$  for *A. xanthophloea* sites as opposed to *A. tortilis* sites, Wald  $\chi^2 = 3.5$ ,  $df = 1$ ,  $P = 0.063$ ). However, only 25 of 124 sleeping sites were *A. tortilis* and only one of the study groups (Weaver’s group) was observed sleeping in *A. tortilis* sites in a portion of their range where *A. xanthophloea* were not locally available. This suggests that *A. xanthophloea* is, overall, a more important sleeping resource than

*A. tortilis* but that *A. tortilis* sites are an important and heavily used resource in the absence of preferred *A. xanthophloea* sites.

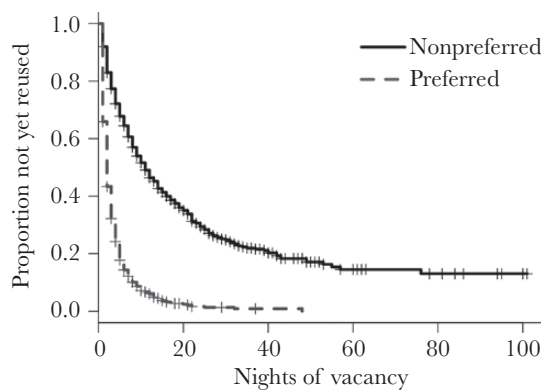
The most dominant group in the study population was significantly more likely than the subordinate group to use sleeping sites with a greater number of trees ( $B = 0.015$ , Wald  $\chi^2 = 95.9$ ,  $df = 1$ ,  $P < 0.001$ ; Figure 4a) and following longer intervals of vacancy ( $B = 0.008$ , Wald  $\chi^2 = 9.0$ ,  $df = 1$ ,  $P = 0.003$ ; Figure 4b).

## DISCUSSION

We found that bouts of continuous sleeping site occupancy for yellow baboons were relatively short, from the perspectives of both single groups and of the entire study population, and for both preferred and nonpreferred sites. At the same time, intervals of vacancy were also relatively short, particularly for preferred sites, which were used almost constantly by the study population as a whole. By highlighting the conflicting interests and behavior patterns of multiple social groups, these results rule out support for any simple version of existing hypotheses for why animals in a wide range of taxa vary their use of sleeping sites rather than consistently using a single site for long periods of time.

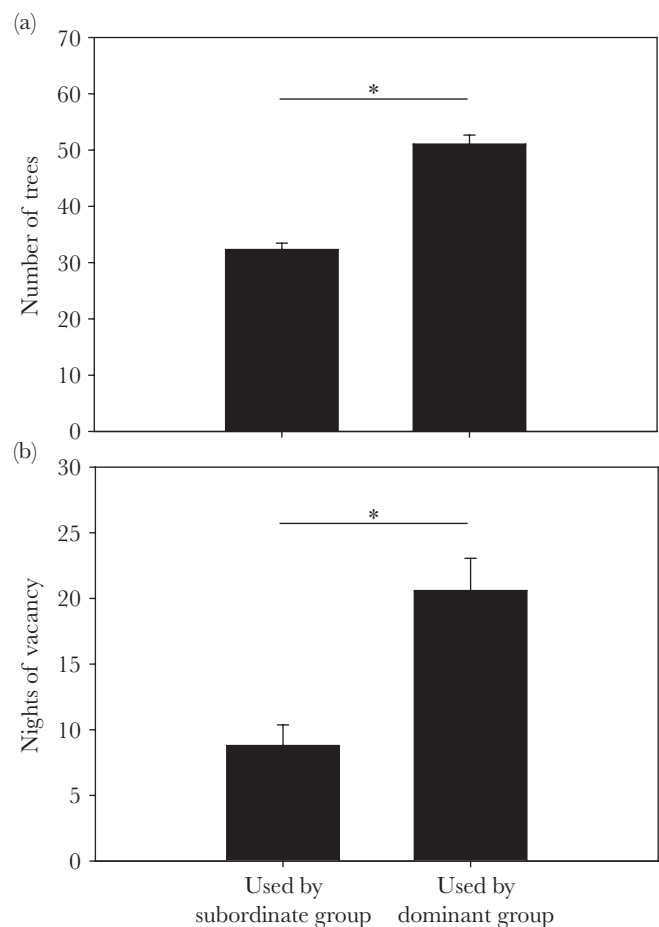


**Figure 2** At the population level, bouts of continuous occupancy at preferred sleeping sites ( $N = 1459$ ) were significantly longer, on average, than bouts of continuous occupancy at nonpreferred sites ( $N = 1542$ ). Crosshairs indicate censored bouts of continuous occupancy.



**Figure 3** At the population level, intervals of vacancy at preferred sleeping sites ( $N = 1428$ ) were significantly shorter, on average, than intervals of vacancy at nonpreferred sites ( $N = 1541$ ). Crosshairs indicate censored intervals of vacancy.

This near-constant occupancy of preferred sites at the population level has important consequences. First, it is likely to facilitate the detection of baboons by predators because these sites become predictable locations of baboons. Despite this higher likelihood of detection, the physical attributes that significantly predicted frequent site use—increased number of trees and healthier trees—suggest that baboons reduce the otherwise potentially high risk of a predator attack by preferentially using sites that offer opportunities for escape if a predator attack occurs. A larger number of trees within a sleeping site may provide safety from predation by 1) increasing the number of arboreal escape routes if a predator attacks (Matsuda et al. 2008) and/or 2) accommodating all members of even large social groups, thus enhancing the probability that a predator will be detected by the baboons, a commonly cited advantage of group living (e.g., van Schaik and van Hooff 1983; Dunbar 1988; Janson 1992; Isbell 1994). In addition, preference for sleeping sites with healthier trees may be attributable to the structural stability of trees in good condition (e.g., Dunbar and Nathan 1972; Bert 1973; Busse 1980). This structural stability is potentially important when baboons retreat to the relatively weaker but safer terminal branches of sleeping trees while under predator attack (Altmann SA and Altmann J 1970; Busse 1980). This suggests that mitigating the baboons’ risk during a predator attack may be a more important



**Figure 4** The most dominant social group in the study population was significantly more likely than the most subordinate group to use sleeping sites with (a) a greater number of trees and (b) following longer intervals of vacancy. Only nights on which the sleeping sites for both of these groups were included in these analyses ( $N = 764$  nights).

consideration in site selection than reducing detection by a predator, perhaps because reducing detection by a predator is somewhat difficult for a large-bodied, gregarious, terrestrial primate.

A second and particularly important consequence of the near-constant occupancy of preferred sleeping sites is the likely increased disease risk through greater parasite transfer between social groups. To avoid infestation from fecal parasites, Hausfater and Meade (1982) predicted that it would be advantageous for baboons to use a particular sleeping site for no more than 2 consecutive nights and to delay site reuse for 8.5 nights, a duration incorporating the time required for larval hatching and subsequent larval mortality. Using data on sleeping site use by a single baboon group in Amboseli during ~200 nights, Hausfater and Meade concluded that the temporal patterns of site use demonstrated a strategy for parasite avoidance. The present study is consistent with Hausfater and Meade's predictions for duration of continuous occupancy at the group level. However, we found that intervals of vacancy even at the group level were often shorter than the predicted optimum. Furthermore, short time intervals until preferred sites were reused by other groups at the population level, despite bouts of occupancy typically less than 3 nights by any single group, resulted in near-continuous occupation of these sites. This implies that groups that share these sites are at high risk for sharing parasites. The high frequency of preferred site use despite these costs raises the question of whether the benefits accrued from using physically high-quality sites offset the risks of parasite exposure; we know of no such evaluation.

On most nights, groups moved to a new sleeping site >500 m from the site used the previous night. However, shorter daily travel distances significantly predicted a group's reuse of the site it had slept in the previous night. Together, these findings offer preliminary support that 1) groups may alternate use among multiple sleeping sites partly to encounter unexploited food resources and 2) reuse of a sleeping site may be an energetically efficient strategy with regard to travel costs as animal's exploit local resources. More thorough evaluation of this hypothesis will require details on the exhaustion and renewal rates of baboon foods and the space-use patterns of neighboring groups. However, even when data on food availability and ranging patterns are obtained, it can be difficult to determine whether sleeping sites are selected because they are in close proximity to food patches or whether animals select sleeping sites and subsequently spend time feeding nearby (Day and Elwood 1999).

How baboon groups detect the recent use of sleeping sites by other groups is currently unknown. Previous research has demonstrated that neighboring baboon groups are rarely in close spatial proximity, despite considerable home range overlap (Markham et al. 2013). Both auditory and visual cues may be important factors mediating this avoidance and, by extension, groups may avoid recently used sleeping sites if a neighboring group has been heard or seen in the site's vicinity. However, these cues are not persistent ones and rather depend on the immediate presence of other groups. Baboons may also rely on olfactory cues to assess recent site use. Hausfater and Meade (1982) hypothesized that odor associated with fecal accumulation beneath sleeping sites, which is even readily detected by humans, may mediate avoidance of sites that have been recently used by other baboon groups.

Evaluating the hypothesis that one benefit of social dominance among groups is priority of access to resources, we hypothesized that the most dominant social group would use a more preferred sleeping site than the most subordinate social group on any given

night. Our findings supported this hypothesis and highlight the importance of social as well as ecological factors in determining optimal patterns of shared resource use: the most dominant group used significantly larger sleeping sites and sites that had been left unoccupied for longer time intervals relative to the attributes characterizing site use by the most subordinate group. This suggests that groups have differential access to sleeping sites, despite long-term sharing, and implies that groups compete for access to sleeping sites. Additional studies on the temporal patterns of site use at the group and population level could evaluate whether encounters between groups at sleeping sites result in a displacement of the subordinate group to an alternative—and potentially less preferred—sleeping site. This would provide valuable insight into how social groups mediate access to shared resources within regions of home range overlap, and the mechanism by which differences in such access affects natural selection and the evolution of sociality.

## SUPPLEMENTARY MATERIAL

Supplementary material can be found at <http://www.behco.oxfordjournals.org/>

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