

Baboon Sleeping Site Preferences and Relationships to Primate Grouping Patterns

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Baboons choose sleeping sites in the following descending order of preference: 1) steep cliff faces and caves, 2) taller emerging trees in continuous forests, 3) the canopy of contiguous forest without emerging trees, and 4) open woodland trees. Choice of sleeping sites in an order appearing to agree with degree of inaccessibility to most predators suggests the hypothesis that predation avoidance is the major basis for use and choice of particular sleeping sites. If this preference order for kinds of sleeping sites is applicable to other large primates, it suggests that spacing of adequate sleeping sites relative to the distribution and density of food resources is one factor contributing to group size and possibly other features of primate social structure. The relatively even distribution of numerous adequate sleeping sites in tropical forests may be one factor permitting evolution of small social units. By contrast, sparse distribution of sleeping sites relative to resource fields may permit the development of large social groups.

Key words: baboons, humans, sleeping sites, predation, resources, Africa, primate, *Papio spp*

INTRODUCTION

Several alternative but not necessarily mutually exclusive hypotheses are available to account for the diversity of social structures [Rowell, 1979] found among primates. Predation often is identified as a selective pressure favoring group formation by diverse species, including primates and other organisms [Hamilton, 1971; Alexander, 1974]. It has also been suggested that primates in savanna environments are more vulnerable to predation because they lack the protection afforded by trees and that this environment has selected for closer aggregation and greater defensive capacity [DeVore, 1962]. The less patchy distribution of food resources in forested environments, especially tropical forests, is suggested to be a correlate and possible determinant of some smaller social groups living there as summarized by Clutton-Brock [1977a, 1977b].

Social structure [Rowell, 1979] of larger primate groups may in part be a consequence of diverse individual self interests of group members. If so, it is unlikely that any single explanation of the characteristics of these species will account for their diverse social

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TABLE I. Habitat Characteristics of Baboons, *Papio* spp., Relative to Alternative Sleeping Sites Available To Various Populations*

	Troop ID	Caves	Cliffs, open	Emerging trees	Closed canopy	Open woodland	Cliffs, wooded	Overhangs	Author
<i>P. ursinus</i>									
South Africa:									
	Northern Transvaal	(+)	+	+		+			Marais, 1939
			(+)	+	+	+			Stoltz and Saayman, 1970
			(+)	[+]					
	RR		(+)	+		+			C. Anderson, pers. comm.
	SH		(+)	+		+			same
	TS		(+)	+		+			same
	AA		(+)	+		+			same
	SE		(+)	+		+			same
	Natal		(+)	+		+			D. Cheney, pers. comm.
	Cape Point		(+)		+				Hall, 1962a, 1963
	O		(+)	[+]	+				Davidge, 1978
	N		(+)		+				same
	S	(+)	(+)		+				same
	Kruger Park		(+)						Saayman, 1971
Botswana:									
	Okavango			(+)	+	+			Personal observations, 1972-1980
	H			(+)	[+]	+			
	G			(+)	[+]	+			
	F			(+)	+	[+ (palms)]			same
	C			(+)	[+]				same
	W			(+)	+	+			same
	Z			(+)	[+]	+			same
	Savuti								Personal observations, 1980
	A†								
	B			(+)	+	+			
	Serondella			(+)	+	+			Busse, pers. comm.

Namibia		+						Hall, 1963
	L		(+)	+	+	+		Personal
	M		(+)		+	+		observations
	U		(+)		+	+		same
<i>P. cynocephalus</i>								
Kenya: Amboseli				(+)	+	[+]		Altmann and Altmann, 1970: S. Altmann, pers. comm.
Tanzania: Mikumi								
	Viramba			(+)	[+]	[+]		R. Rhine and G. Norton, pers. comm.
	VI			(+)	[+]	[+]		same
	VII			(+)	[+]	[+]		same
	VIIs			(+)		[+]		same
	Mgoda			(+)	[+]	[+]		same
<i>P. papio</i>								
Senegal	S2			(+)	+	+		Dunbar and Noonan, 1972
	S4			(+)	+	+		same
	S5			(+)	+	+		same
			(+)	+	+	+		Bert et al., 1967
<i>P. hamadryas</i>								
Ethiopia		+	(+)	+	+	+	+	Kummer, 1968
<i>Theropithecus gelada</i>								
Ethiopia			(+)					Crook, 1966
<i>P. anubis</i>								
Tanzania: Gombe				(+)	+	+	+	Ransom, 1971
				(+)	+	+	+	same
Uganda	S			(+)	+	+	+	Rowell, 1966, 1972
	U			(+)	+	+	+	same
Kenya: Gilgil			(+)	+	+	+		Smuts, pers. comm.
				(+)	+	+		same

*No entry means site type is unavailable or unreported for that troop. A plus sign means the site type is present but not recorded as used for sleeping. Preferred site types are indicated by a plus (+) sign and the less frequently used site type is indicated with [+].

†Preferred to roost in dead tree snags over open water.

characteristics. Many selective pressures probably operate to differing degrees upon each species, accounting for the diversity of social structure and organization [Rowell, 1979] often found in similar habitats. Spacing of suitable sleeping sites relative to the distribution of foraging areas is one such determinant considered in this paper.

METHODS

Characteristics of alternative kinds of baboon (*Papio* spp.) sleeping sites are analyzed here. For brevity, the species of baboon is identified in Table I and in the text only where the species is not evident. (Blanks in Table I represent either absence of sleeping sites of that sort or a lack of information.) Baboons are chosen for comparison because they occupy diverse habitat types, choose diverse sleeping sites with various physical characteristics, and because descriptive observations for a large number of populations are available. The extent of analysis is limited because observations were not systematically obtained with the question of sleeping site choice in mind. Evaluations and explanations here are intended to review these observations and provide a set of hypotheses.

Sleeping Site Characteristics

Sleeping sites are allocated to several categories further identified schematically in Fig. 1. These categories are:

Caves. These are defined as recesses over 5 m deep into rock faces. Two kinds of caves are distinguished: those with entrances at the base of cliffs and those with entrances above bases on the faces of cliffs (Fig. 1).

Open Cliffs. Open rock faces free of extensive woody vegetation sloped to within 20° of the vertical are included in this category. Rock faces with slopes of less than 70° are not reported as used by baboons for sleeping sites at any locality.

Wooded Cliffs. Unlike open cliffs, the face of wooded cliffs can be reached by baboons, and predators such as climbing cats from trees adjacent to or growing on the cliff. Such sites are characteristic of some mesic tropical forest environments, but they are not reported as used by baboons for sleeping.

Emerging Trees. Degree of emergence above the surrounding canopy varies and is, for sleeping groves used by baboons, never as extensive as that of true tropical forest emerging trees, which protrude well beyond the canopy. Emerging trees as considered here may rise only slightly above the adjacent forest and the contour of the canopy may taper to the level of adjacent forest trees (Fig. 2). The emerging trees used as sleeping sites by baboons tend to have characteristics other than height distinguishing them from the adjacent forest. Their structure is often relatively open below the crown, and large lateral limbs provide vertical and horizontal access for baboons to the rest of the tree and to adjacent trees.

Closed Canopy. Closed canopy as defined here includes canopies which can be traversed by baboons without return to the ground. The category contrasts with emerging trees in that the canopy is relatively even, and strong vertical and horizontal structuring are not present.

Open Woodland. In these habitats movement to adjacent trees by baboons is not possible without return to the ground. Baboons may be less agile and acrobatic than other species of monkeys, especially forest-dwellers, but the degree of difference is in most cases relatively slight, and operationally open woodland is almost the same for other monkey species in terms of ability to escape from predators by moving to adjacent trees (Fig. 3). Patas monkeys, *Erythrocebus patas*, are a notable exception. They are highly differentiated for high-speed flight in open terrain, and their choice of dispersed woodland sleeping groves may be related to their great ability relative to other monkey species to escape by running on the ground.

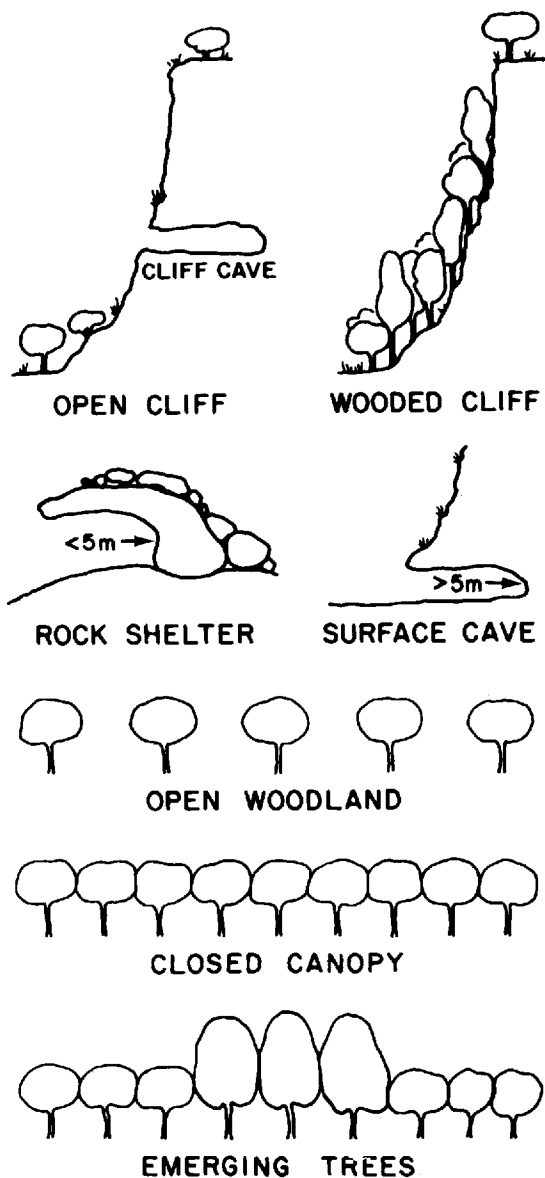


Fig. 1. Profile characteristics of alternative savanna baboon sleeping sites. There are no reports of wooded cliffs being used as sleeping sites.

Rocky Overhangs. Rock shelters, such as those widely used by Bushmen and probably numerous other prehistoric human populations, are not reported as used for sleeping by baboons. These sites may be, but are not necessarily, elevated above the surrounding terrain. Distribution of depths vary, overlapping the characteristics of caves as defined above. Rock overhangs are defined here as being no deeper than 5 m.

Descriptions of primate field study areas often provide limited information about specific habitat characteristics. Hence, observations of sleeping site characteristics re-



Fig. 2. A typical sleeping site for chacma baboons in the Okavango Swamp, Botswana. The *Acacia nigrescens* trees in the center of the photograph rise above the closed canopy and are strongly structured vertically and horizontally, permitting lateral movement at night. The palms,

Hyphaene ventricosa, were never used at this site but are used by other troops of chacma baboons when more suitable emerging canopies are not available.



Fig. 3. Seasonally used as a foraging area, this *Mopane calophospermum* forest includes both closed and open canopies. Chacma baboons foraging

long distances from more preferred sleeping sites such as that shown in Fig. 2, occasionally use dense portions of this forest as a sleeping site.

ported here are incomplete. Since the comparisons here are made only for kinds of sleeping sites known to be present, this limitation should not introduce a directional bias into the analysis.

RESULTS

Sleeping sites personally observed and described in the literature as used by baboons are allocated when appropriate to one of the above categories. In addition, the availability of the other categories of sites is reported. A summary of this analysis (Table I) shows the category of sleeping sites chosen by baboons as determined by the greatest frequency of use during the interval of observations.

The sample size for analysis is based upon troops as units of measurement. Troops of a local population may be influenced by one another in their choice of sleeping sites. However, since there is often variation in the kind of site chosen by a single troop, it is assumed for purposes of this analysis that each troop exercises choice according to all available alternatives. The preference of a large number of chacma baboon troops for cliffs as sleeping sites in the northern Transvaal, South Africa, may be a local tradition. But Stoltz and Keith [1973] report use of emerging trees in that area, both exclusively for some troops when no cliffs are present and occasionally when both cliffs and emerging trees are present. Stoltz and Keith's [1973] specific observations are not entered in Table I because they reported no information on preference for alternatives.

For a limited number of sites (four) where caves are present, they are chosen equally with cliff faces. Location of caves at cliff bases as opposed to faces does not preclude their use [Hall, 1962, 1963]. Where open cliff faces are present and caves are not, cliffs are preferred to emerging trees as sleeping sites (12 choices of cliffs, no choice of emerging trees, $P < 0.001$). Emerging trees follow in the preference order and are chosen over closed forest canopies when both habitat types are present (23 emerging trees, 0 preferences for closed canopy when both are present, $P < 0.001$). Open woodland sites are seldom used for sleeping and are never reported as the sleeping site of choice when emerging trees are also present (22 emerging trees, 0 preferences for open woodland, $P < 0.001$).

The only exception to a perfect fit of preference ranging downward from cave-cliff, emerging trees, closed canopy, and open woodland is the single observation of the F troop, Botswana, which chose scattered palm trees over shorter closed canopy. Guy Norton reported four troops using both closed and open sites at Mikumi, Tanzania, but did not indicate which were preferred.

Some individual sleeping sites contain a mixture of site types according to the criteria of Fig. 1. In Botswana, the Z and C troops both used a site which included two emerging tree species and numerous palm (*Hyphaene ventricosa*) trees, some adjacent to one another, others isolated to the extent that lateral canopy movement was not possible. Isolated palms were most commonly used by independent two- to three-year old juveniles at this site. Adjacent palms and the emerging trees were used by adults and female-infant subgroups. This same palm species at roosts with more suitable characteristics, as shown in Fig. 2, were not used for sleeping. The F troop, Botswana, also occasionally used a palm tree roost lacking other substantial trees. There, numerous isolated palms were used at night by all age/sex troop members. Their most heavily utilized roost was, however, an emerging *Acacia nigrescens* copse in another part of their home range.

At the Savuti Marsh, Botswana, a troop of chacma baboons regularly used dead acacia trees in the now flooded Savuti Channel, a slow moving, shallow, 20 m wide river. This sleeping site does not fall into any of the categories of sleeping sites described above. Some individuals swam to these snags, then climbed into them to spend the night. Other individuals crossed water on fallen logs to reach the sleeping snags. Little or no lateral movement was possible in these dead trees. But the site probably afforded good protection from leopards, who were observed chasing baboons coming to roost at this site. This

special situation emphasizes the facultative response of baboons to roosting opportunities.

Preferences identified here may reflect traditional choices of sleeping sites which have been relatively free from predators. Following nocturnal attacks by leopards we observed troops changing roosts, after they had used a particular roost on several previous nights.

The observation reported above of baboons roosting on dead, leafless and open snags in the Savuti Channel identifies another common characteristic of many baboon sleeping sites – their openness to the ambient environment. Baboons may choose wooded thickets with dense foliage if they also satisfy the structural characteristics described here. But they also frequently choose the upper reaches of trees with light foliage or with no leaves at all. Cliff sites generally are completely open to wind and may provide little or no overhead protection.

The response by unhabituated baboons to human observers at night is to move laterally to adjacent trees while remaining in the canopy. On open cliffs in Namibia, movements were less extensive in response to disturbance by spotted hyenas and humans, and cliffs were never abandoned at night. The ability of baboons to move in trees and on cliffs is generally greater than that of their predators. Nocturnal leopard predation is a major basis of baboon mortality [Busse, 1982], and the vulnerability to leopards and other predators should be greatest at the least preferred sleeping sites, but no data are available to test this prediction.

DISCUSSION

Observations of baboons under attack by predators at sleeping sites are limited. There was a general vocal alarm and some stone releasing [Hamilton et al., 1975a] by baboons sleeping on cliffs in the Namib in response to spotted hyenas. In trees, individuals are quick to move laterally if a leopard or a human walks under the roost tree, and move to the ends of branches or to adjacent trees when pursued in tree roosts by leopards [pers. obs.]. The potential for escape without return to the ground is probably the basis for choice of relatively strongly structured tree roosts.

The ability of baboons to scale rock faces and move through the forest canopy has not been the subject of any detailed analysis. Given the reputation of these species as “ground-dwelling” primates, their climbing ability is remarkable, appreciably better in most circumstances than that of cats, who can not use finger holds to move up the kind of sheer cliff faces scaled by baboons.

The potential to escape through the forest canopy or to relatively inaccessible places on cliffs is the most probable basis for the choice of sleeping sites with particular characteristics. Behavior of predators and baboons at sleeping sites has never been the subject of extensive observation. Marais' [1939] single dramatic report of two adult male chacma baboons confronting and killing a leopard on a South African cliff needs confirmation.

Observations of chimpanzees, *Pan troglodytes*, attacking red colobus monkeys, *Colobus badius*, in forest canopies suggest that for this species pair the balance tips in favor of the predator only in open forest canopy environments, when the potential for lateral, arboreal movement by colobus monkeys is limited [Wrangham, 1975]. This relationship and the possibly greater ability of cats and other predators to move about at night may contribute to the effectiveness of nocturnal predation upon baboons by leopards.

Use of sleeping sites with less desirable characteristics may be based upon the distance of foraging areas from more favorable sleeping sites. This hypothesis suggests that when foraging conditions are less favorable and when more of the home range is utilized, the frequency of use of less suitable sites will increase.

Sleeping sites are not easily defended from other troops because they are large and usually three dimensional. Troops at some localities do exclude others from sleeping sites [Hamilton et al., 1975b, 1976], but mutual use of the same or adjacent sleeping sites

by troops has also been reported [Kummer, 1968; Hamilton et al., 1976; Rowell, 1966]. Encounters between troops at sleeping sites may result in displacement of one group to an alternative sleeping site or to a less preferred site. For Okavango Swamp troops (N = 18), this invariably resulted in the losing troop moving to a closed canopy roost from an emerging *Acacia nigrescens* roost (pers. obs.).

The significance of sleeping site distribution to primate social organization has been considered for hamadryas, *Papio hamadryas* [Kummer, 1968], and gelada baboons, *Theropithecus gelada* [Crook, 1966; Dunbar & Dunbar, 1975; Kawai, 1979]. These species show strongly differing patterns of nocturnal aggregation and broadly similar patterns of social subunit structure. Thus, sleeping site characteristics should be viewed as a constraint upon patterns of social grouping rather than a determinant of them.

Trees are widely used by primates as nocturnal roosts, and riparian forests, sections of which agree with the definition of emerging trees used here (Fig. 1), are used by a diversity of macaques and langurs as sleeping sites. If nocturnal predation is a selective force favoring use of sleeping sites relatively immune from predation, in those environments where such sites are relatively numerous and evenly distributed, such as in tropical forests, small groups become possible.

This suggestion contrasts with other hypotheses relating aggregation to predation: 1) that large groups of primates characteristic of woodland and savanna environments require active group defense against diurnal predators [DeVore, 1962]; 2) that the large numbers of individuals in such groups minimize individual risk because of the probability that a predator will be seen earlier [Armitage & Downhower, 1974; Sherman, 1977; Wittenberger, 1979]; and 3) that large group size reduces the risk to individuals of being captured by a predator [Hamilton, 1971].

None of these hypotheses, including that presented here, are exclusive alternatives. But the relationship of sleeping sites to group size and possibly to social organization has not previously been identified and may favor aggregation as much as or more than selection based upon previously identified alternatives. Tropical forest environments also are occupied by primate species characterized by larger groups, so the distribution of sleeping sites in such environments can be considered only as a permissive condition for development of small groups.

During one interval, a relationship of resources to choice of marginal sleeping sites was apparent. An Okavango Swamp troop was alternating between only two sleeping sites, both with extensive emerging *Acacia nigrescens* trees. During an outbreak of a favored food, scale insects [Hamilton et al., 1978], the troop moved daily deep into a mopane forest, the host tree for this insect. When this food occupied over 50% of this troop's foraging time, they chose to roost (seven times) in the mopane forest, a forest clearly definable as closed canopy (Fig. 2). On other occasions when the mopane forest was used for scale insect foraging (42 occasions), the H troop returned to one of the two preferred emerging tree sleeping roosts. When mopane scale insects were not available, this troop did not use closed canopy roosts.

Use of caves as sleeping sites is based upon limited evidence because of the small number of such sites available to and/or occupied by baboons. If such sites are indeed preferred, it can not be for the same reasons that other sites are preferred, i.e., invulnerability and ease of escape, which appear to be the basis for choice of cliffs and trees as sleeping sites. Caves may be chosen because of their defensibility. A small number of individuals could effectively blockade the mouth of a cave against one or more predators. This is not the case for the other categories of sleeping sites. Since there are no reported observations of baboons responding to the intrusion of predators into caves occupied by baboons, this remains speculative.

Hominid Shelters

The importance of caves in hominid evolution is not easily evaluated because of the probability of differential preservation of human artifacts found in caves and other rock

shelters. If use of caves was accompanied by the development of unique defensive capability, the importance of such sites to human evolution may have been particularly great. Rock overhangs, one form of shelter used by Recent Bushmen and other Recent hunter-gatherers, are not used by baboons for sleeping.

Hominid use of rock overhangs as sleeping sites is without counterpart among other primate species. Analysis here of baboon sleeping sites emphasizes the importance of inaccessibility to and flight from predators as a probable basis for choice of sleeping sites by baboons and probably other primates. Such sites usually are not actively defended against predators [but see Marais, 1939]. By contrast, rock shelters used by humans are relatively accessible to a variety of predators, suggesting that occupation of such sites depended upon developments reducing vulnerability to predation and making possible active as opposed to passive defense. Rock overhangs could only be defended actively, as opposed to passively, the general response of baboons to predators at sleeping sites. Use of such sites seems to imply social cohesion and a potential for active defense.

Because the dichotomy between active defense and flight has been overlooked in limited, previous discussions of primate sleeping sites, the significance of use of caves, sites seemingly suited only to active defense, as nocturnal roosts by primates has not been closely considered. Studies of such sites when primates are under attack by natural predators are of considerable significance to evaluation of primate group cohesion and the development of early hominid responses to predators.

Geist [1978] has discussed the shift from stalking hunting [*sensu* Hamilton, 1973] to direct confrontation of predators, identifying the timing of such a development as correlated with the emergence of *Homo erectus* and stone weapons associated with this human ancestor. It is possible that a change in hunting tactics to include group hunting, and especially the ability to confront as opposed to stalk prey, was also associated with development of characteristics making active defense of relatively vulnerable sleeping sites possible.

Regardless of when the potential to effectively and cooperatively defend against predators occurred in human evolution, it may have coincided with adoption of sleeping sites with characteristics other than those used by contemporary baboons, making possible more extensive use of the ground and defensible shelters.

CONCLUSIONS

1. Baboons select nocturnal roosts with characteristics which suggest that choices of alternatives are based primarily upon their degree of security from predation.

2. Sites chosen, in decreasing order of preference, are steep cliff faces, emerging trees, closed canopy forest trees and open woodland trees (Fig. 1). Free-ranging baboons have never been reported to sleep on the ground.

3. Caves appear to be chosen as sleeping sites at certain locations and may be favored. Details of the characteristics of such caves and patterns of defense against predators have not been reported, with one possible exception. Comparison with aboriginal human sleeping sites in rock shelters suggests that when such sites were first successfully occupied, the occupants were able to effectively defend themselves.

4. Rock shelters such as those used by some prehistoric and aboriginal humans (Fig. 1) are not reported as used by baboons, presumably because use of such sites requires more effective defense against predators, available to humans but not to baboons.

5. Extension of the sleeping site preferences described in this paper to other primates spending the night in trees suggests that the distribution of resources relative to adequate sleeping sites may be a relationship determining the potential to adopt alternative primate grouping characteristics. Sleeping sites are not highly defensible from other individuals and groups, and aggregation of subgroups at localized but highly desirable sleeping sites may lead to sleeping aggregations. By comparison, the strong vertical and lateral structure of tropical forest canopies may provide a surfeit of sleeping sites, making possible the autonomous existence of numerous small social groups. It is not sug-

gested that sleeping site characteristics and distribution determine the character of social units, only that sleeping site characteristics may make certain social grouping patterns possible.

6. The relationship of sleeping sites to predation defense identified here suggests that in tropical forests suitable sleeping trees may be evenly dispersed, a condition permitting multiple forms of spacing patterns relative to food resources.

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