

## Characteristics and Use of Sleeping Sites in *Aotus* (Cebidae: Primates) in the Amazon Lowlands of Peru

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In the Amazon lowlands of Peru, *Aotus nancymai* and *A. vociferans* were observed to use four different types of sleeping sites: 1) holes in the trunks and branches of dry or senescent trees; 2) concavities in polyaxial branching nodes of trees protected by dense entanglements of creepers, climbing plants, vines, and masses of diverse epiphytes; 3) complex sites among masses of epiphytes, climbers, and vines; and 4) simple sites among thickets and dense foliage. Each type is described. There was competition and sharing of sleeping holes between *Aotus* and other nocturnal arboreal mammals.

**Key words:** *Aotus nancymai*, *Aotus vociferans*, forest strata

### INTRODUCTION

All neotropical nonhuman primates are diurnal with the exception of *Aotus*, which is nocturnal. Prior to 1982, all studies of *Aotus* in natural areas referred to *Aotus trivirgatus* as the only species occurring in South America. Hershkovitz [1983] recognized the existence of nine species of the genus *Aotus*. With the description of *Aotus hershkovitzi* by Ramirez-Cerquera [1983], the number of species of *Aotus* has been increased to ten.

Napier and Napier [1967] and Wright [1978, 1981] described the daytime sleeping sites of *Aotus* as tree holes, entanglements of climbers and vines, and thickets of bamboos and vines. Wright based her observations on a family group living in a hillside forest along the Pichis River near Puerto Bermudez, Department of Pasco, Peru. Hershkovitz [1983] described the daytime sleeping sites of *Aotus nancymai* as lacking any sign of intentional construction in trees or in entanglements of climbers and vines supported by the branches of large trees. Coimbra-Filho [1977], in a study of the ecology of *Leontopithecus rosalia*, described the use of tree holes as refuge from predators and for resting or nighttime sleep. *Aotus* and *Leontopithecus* are the only neotropical primates that sleep in holes in the trunks of trees.

We located and examined the sleeping sites of 77 family groups of *Aotus*. Following Hershkovitz [1983], 42 groups were *Aotus nancymai* and 35 were *A. vociferans*, including a new karyotype among the "grey neck species group" of Hershkovitz [Ma et al, 1985]. Family groups of *Aotus nancymai* were located in the

Received January 21, 1986; revision accepted July 15, 1986.

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forest along the Tahuayo River. Family groups of *A. vociferans* were studied along the Nanay and Napo Rivers. These study sites were in the Department of Loreto. Our long-term observations (1981–1983) have shown that *Aotus* sleep from between 0500–0550 hours to 1800–1835 hours (local time) while hidden in sleeping sites located in holes or concavities in trees or among entanglements of climbers, vines, epiphytes, and other dense foliage. Other arboreal and nocturnal mammals such as *Potos flavus*, *Bassaricyon gabbi*, *Isotrix villosa*, *Coendu bicolor*, and bats use sleeping sites similar to, or the same as those of *Aotus*, often with indirect competition or time-sharing.

## STUDY AREAS

The study areas were located 1) along the middle course of the Napo River between Santa Maria, Santa Clotilde, and Puerto Huamán; 2) along the lower course of the Nanay River between Lagunas, Yarina, and Mishana; and 3) in the vicinity of Huaisi along the lower course of the Tahuayo River (Fig. 1). Observations were made from canoes and were concentrated along the river and the ox-bow lake or “cocha” margins and in the proximity of small feeder streams.

The architecture of vegetation, the soil, and the effects of seasonal fluctuations in water level and human activities varied within the study areas. The different levels or strata in the Amazonian forest vegetation are readily apparent because different floristic elements have uniform physiognomic characteristics [Ducke & Black, 1954; Pires, 1974; Prance, 1979; Encarnación, 1985].

At Huaisi the soil is muddy and of recent alluvial origin. There is no topographic relief, and the area is flooded successively by black, mixed, and white water during a single flood stage. These characteristics determine the floristic composition of the “Tahuampa” forest [Encarnación, 1985], which includes among other plant species *Hura crepitans*, *Couroupita subsessilis*, *Clarisia biflora*, *Chorisia insignis*, *Campsiandra* spp., and *Macrolobium acaciaefolium*. These species attain heights greater than 25 m, and since they have commercial importance as lumber, both the structure and height of the plant cover have been altered by selective logging. It is possible, nevertheless, to distinguish several strata. There is a lower story of dense, woody understory between 8 and 10 m in height and a middle story between 11 and 15 m, with thin and tortuous trees supporting climbers and semiwoody vines. The uniform upper story is between 16 and 20 m high and consists of large trees and entanglements of climbers and vines. In places, this upper story is interrupted by an older, higher story between 21 and 25 m in height consisting of old, partially fallen senescent trees, supporting vines, hemiepiphytes, and woody epiphytes. Among this emergent level, some trees attain 40 m in height.

Along the Nanay River, the soil is clay-like mud and is of older alluvial origin. The relief is slightly undulating, and low areas are inundated by both black and mixed water. The riparian forest is of the black-water “tahuampa” type described by Encarnación [1985]; it is composed of *Eschweilera* spp., *Campsiandra* spp., *Pithecellobium laetum*, and other species of large size and height, which are without commercial value. The understory is dispersed and composed of shrub between 10 and 15 m high. The middle story consists of mature tree trunks between 16 and 20 m in height. The upper story presents a uniform aspect with mature, senescent, and dead trees between 21 and 30 m in height, which support lianas, hemiepiphytic vines, and some herbaceous epiphytes. The emergent trees reach almost 40 m in height and sometimes form a diffuse stratum that supports many epiphytes.

Along the Napo River, the soil is muddy and of recent alluvial origin; the topography is somewhat undulating, and the terrain is inundated seasonally by white water. The forest is of the “tahuampa” type represented by *Calycophyllum*

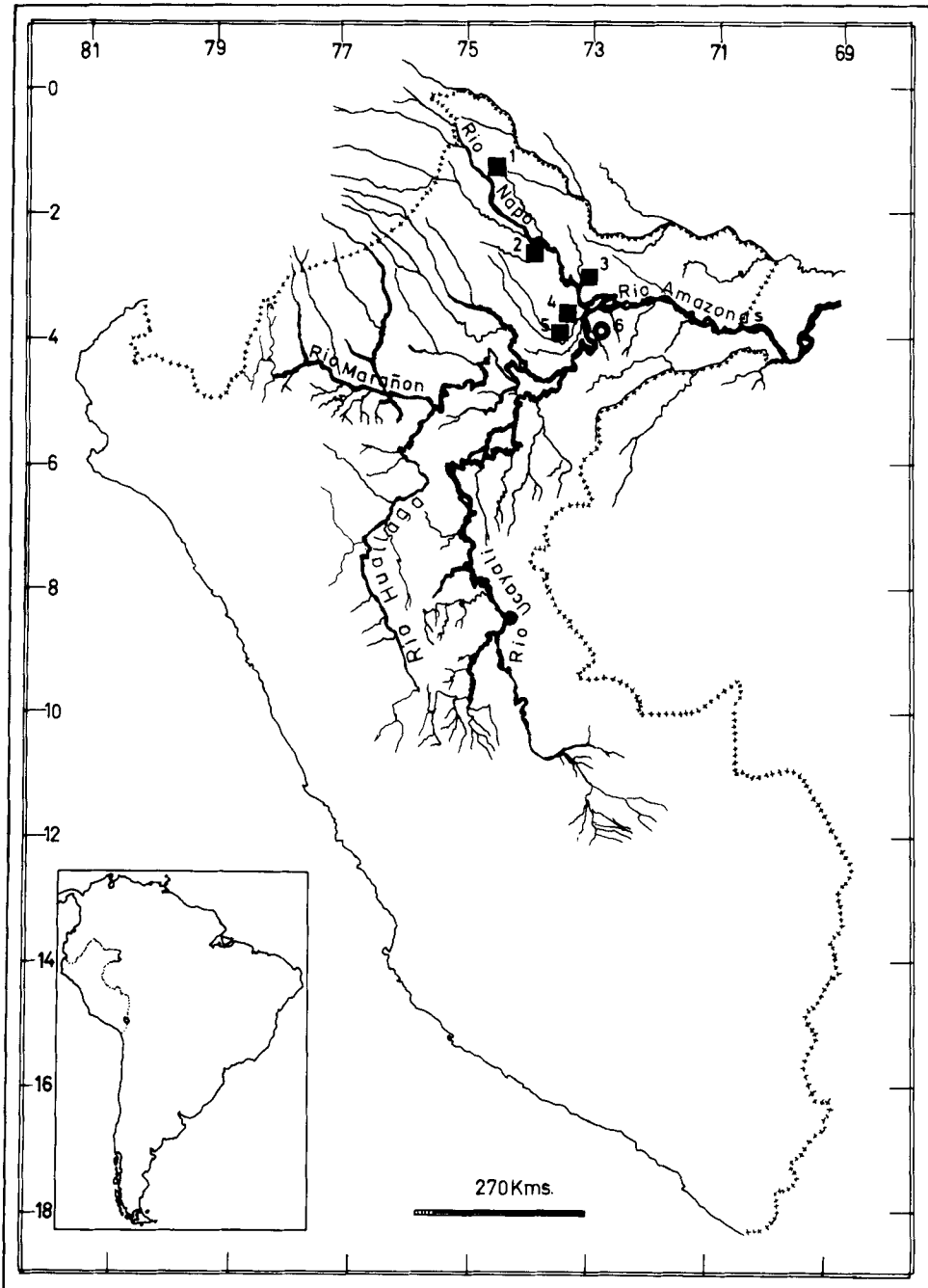


Fig. 1. Map of Peru showing the study areas. (■) *Aotus vociferans*: 1. Santa María, 2. Santa Clotilde, 3. Puerto Huamán, 4. Mishana, 5. Yarina. (○) *Aotus nancymai*: 6. Huaisi.

*spruceanum*, *Naucleopsis glabra* and *Naucleopsis imitans*, and *Scheelea* spp., in associations called "capironales," "tamamurales," and "shapajales." These species attain great height but have no commercial value. The understory is composed of thin and erect trees between 10 and 15 m high, without thickets. The middle story consists of straight and erect trees reaching from 16 to 20 m in height, with few vines or climbers. The upper story, between 21 and 30 m, consists of the foliage of low branches, which support dense entanglements of climbers and vines. Emergent trees reach over 40 m. In some places, stands or associations of mature, senescent, or dead emergents define a true upper story.

## METHODS

Family groups and sleeping sites were located by direct sighting during dusk and predawn censuses. Censusing was carried out from 1800 to 2030 hours and between 0300 and 0600 hours. Dusk censuses facilitated the location of groups, while dawn censuses facilitated the location of sleeping sites.

The height, form, composition, and characteristics of the sleeping sites were recorded. These observations were made at the sites by the principal author with the aid of a field assistant trained in tree climbing. Repeated observations were made of the use of the sleeping sites by *Aotus* and by other arboreal nocturnal mammals. The collection and analysis of biological samples included insects, plants, and some organic remains.

## RESULTS

### Principal Types and Forms of Sleeping Sites

Sleeping sites included 1) holes and concavities in trees, 2) climbers and vines supported by trees, 3) masses of hemiepiphytes and hemiparasites, and 4) thickets and dense branches of shrubs and bamboos (Fig. 2). These four primary types of sleeping sites comprised eleven different or variant forms.

**Type A.** Sleeping sites are in holes of tree trunks. Access is by the thin trunks and branches of neighboring trees, climbers, or vines. This type of sleeping site affords optimal conditions of shelter and security from predators.

**Form Aa.** This form is the apical position in the dry trunk of a palm (generally *Scheelea* spp., *Guilielma gasipaes*, or *Mauritia flexuosa*), whereby entrance is gained by the trunk or some proximal leaf. The superposition of branches and leaves of adjacent trees prevents the direct entry of rainwater into the hole (Fig. 2Aa).

**Form Ab.** This form is the apical position in the trunks of dry or senescent trees that can have "reiterations" [sensu Halle et al, 1978]. The entry of rainwater into the hole is prevented by the superposition of the branches of taller neighboring trees (Fig. 2Ab).

**Form Ac.** This form is the subaxial position on senescent or dry trunks where the entrance corresponds to the knot of a fallen branch (Fig. 2Ac).

**Form Ad.** This form is the subapical position with one or more entrances in dry or senescent trunks. Woody epiphytes whose roots reach into the cavity and form steps or shelves are used by *Aotus* for resting or daytime sleep (Fig. 2Ad).

**Form Ae.** This form is the lateral position over thick, dry, or senescent branches of trees *Macrolobium* sp., *Eschweilera* sp., and *Calycophyllum spruceanum* (Fig. 2 Ae).

**Type B.** These complex sleeping sites are in the concavities of branches supporting entanglements of climbers and vines, which serve as access routes and provide protection and shelter. Branching patterns are principally of the Koriba, Prevost, or Nozeran models [Halle et al, 1978].

**Form Ba.** This is an axial concavity formed by more than four branches (Fig. 2 Ba).

**Form Bb.** This is a subaxial concavity formed by the loss or fall of a branch (Fig. 2Bb).

**Type C.** These complex sleeping sites are composed principally of epiphytes, hemiepiphytes, and hemiparasites (Bromeliaceae, Araceae, Loranthaceae, Guttiferae, Moraceae, Gesneriaceae, ferns, and others), almost always in parabiosis with ants. Access is by vines or by the branches of neighboring trees.

**Form Ca.** This form is the subaxial position over a slight concavity protected by diverse epiphytes and hemiepiphytes. The concavity is produced by the fall of a branch in the Nozeran model [Halle et al, 1978] (Fig. 2Ca).

**Form Cb.** This form is the subapical position without concavity. The sleeping site is at the base of the diverse epiphytes and hemiepiphytes that grow on a palm of the intermediate model of Holtum and Corner [Halle et al, 1978] (Fig. 2Cb).

**Type D.** These simple sleeping sites are positioned among thickets and dense foliage with multiple or defined access.

**Form Da.** This form is the axial position with protection provided by the foliage of branches of trees principally in the models of Aubreville, Mangenot, or Massart [Halle et al, 1978] (Fig. 2Da).

**Form Db.** This form is the irregular position with protection from foliage and thickets of dense shrubs or trees with poliaxial branching, as occurs in bamboos of the McClure model or Myristicaceae of the Aubreville model [Halle et al, 1978] (Fig. 2Db).

The form Ac, characterized by the presence of epiphytes and woody hemiepiphytes (*Ficus* sp., *Coussapoa* sp., *Clusia* sp., *Souroubea* sp., and others) with root systems rooted in the holes, can be confused with form Bb when they are covered by herbaceous or semiwoody climbers (Bignoniaceae, Vitaceae, Cucurbitaceae, Menispermaceae, Convolvulaceae, and others) and some succulent and herbaceous epiphytes.

In dry or senescent trees, the orientation of the cavity is generally descending with respect to the entrance or opening. However, in the forms Aa and Ad, it can occur with an ascending orientation. In forms Ba and Bb, protection from rain is complemented by the foliage, the decomposition and detachment of cork, and the desintegration of arthropod and other remains, which are sometimes the substrate of certain epiphytes (Araceae, Bromeliaceae, Cyclanthaceae, Gesneriaceae, etc).

In form Ca, the foliar scars and the spathes of palms such as *Scheelea cephalotes*, *S. bassleriana*, and others called "shapaja" constitute the base of the sleeping site, whose form is then complemented with *Philodendron* sp., *Ficus* sp., *Polypodium* sp., and *Nephrolepis* sp. among the epiphytes.

The form Da is frequent among small trees of *Rheedia* sp., *Ocotea* sp., *Iryanthera* sp., *Cordia* sp., *Sapium* sp., and others, while the form Db is found over thickets of *Guadua superba* in Loreto Department and over *Guadua* sp. between the Manuripe and Acre Rivers in Madre de Dios Department.

### Description of Sleeping Sites

Tree holes were the most common sleeping sites of *Aotus nancymai* and *A. vociferans*. These cannot, in any way, be properly considered built nests. Other nest types, which lacked walls, were also unmodified. Tree holes were characterized by one to three orifices or access routes into the internal cavity. We have rarely found holes with four or five orifices and have found them only in trees of *Calycophyllum spruceanum*, *Campsandra laurifolia*, and *Eschweilera* sp. However, only one or two

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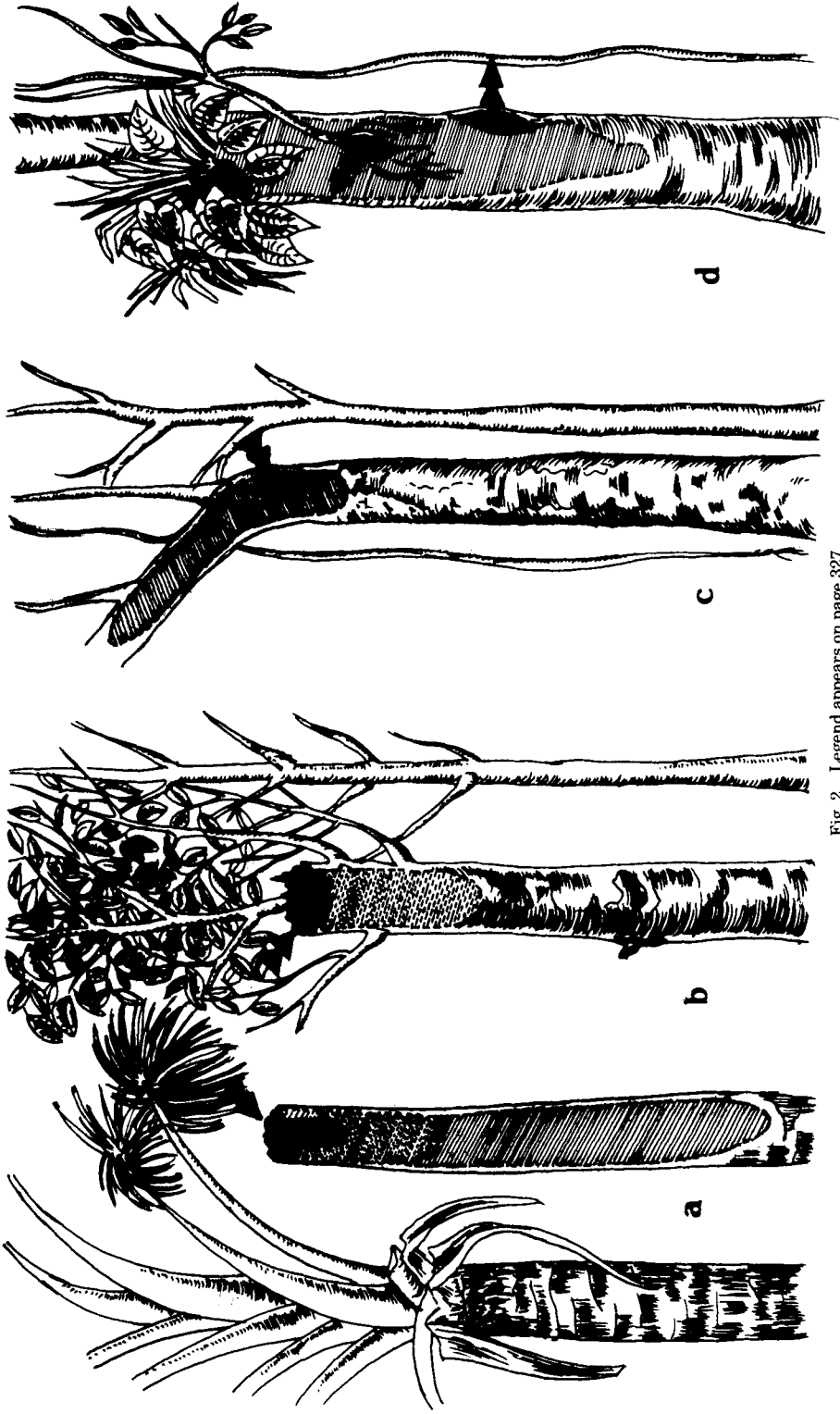


Fig. 2. Legend appears on page 327.

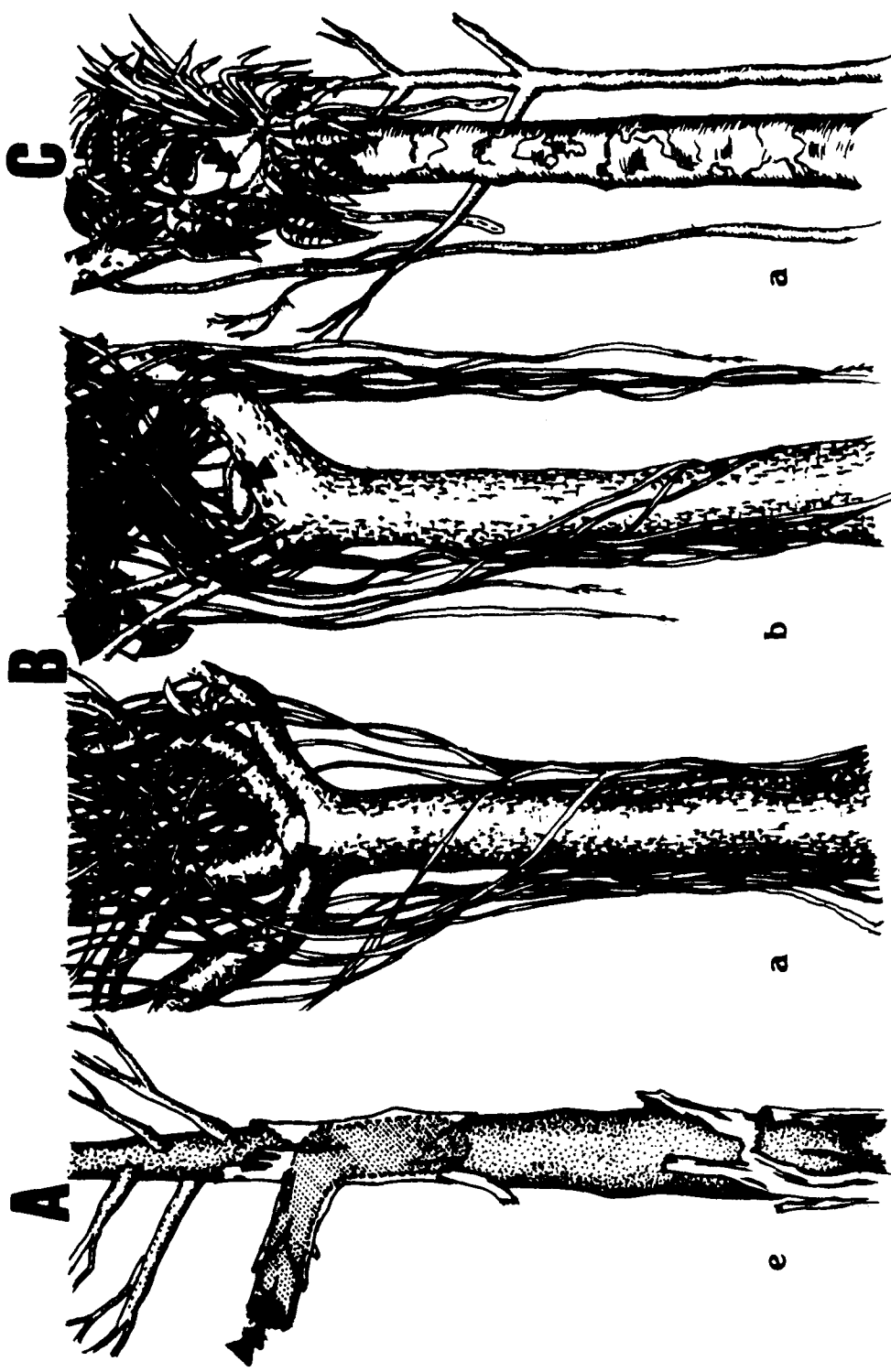
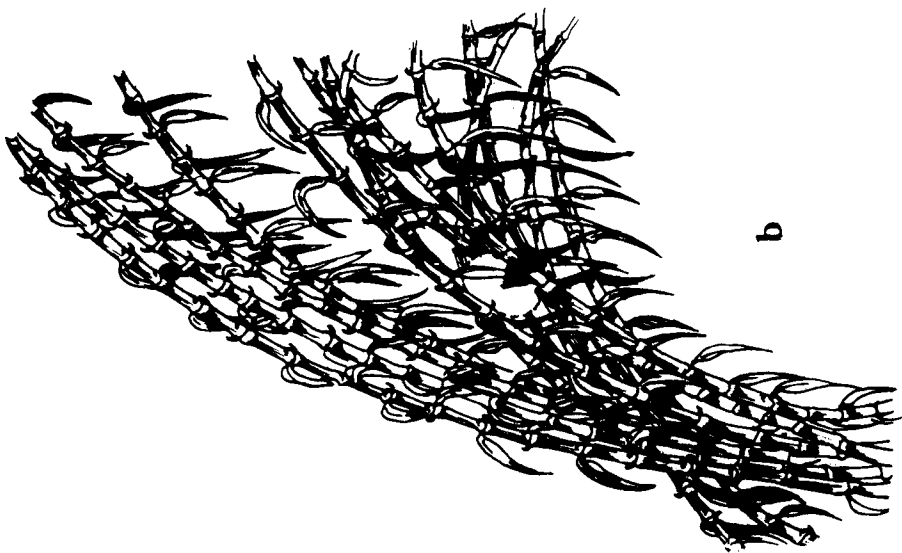
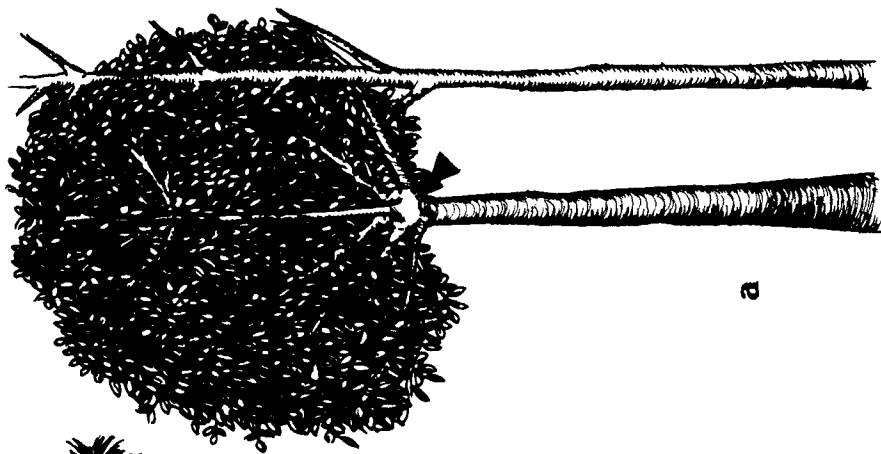


Fig. 2. Continued.



**D**



**C**





of these routes were used by *Aotus* for routine entries and exits; the others were used only circumstantially. Access holes were generally almost circular, with diameters varying between 14 and 30 cm.

The internal cavity was generally cylindrical in form, having the same or a somewhat larger diameter than the orifice. The depth of the cavity varied between 0.6 and 13.4 m. Some cavities contained roots of hemiepiphytes and hemiparasites that formed steps on ladders for *Aotus*. Generally, the cavity was clean and more or less dry. Organic remains, if they existed, were found at the bottom of the cavity in the process of decomposition. These remains served as substrate for fly larvae and other insects. The walls of the internal cavity and orifice showed wear and polish as a result of the constant traffic of individuals. These walls were impregnated with odoriferous substances secreted by the subcaudal and pectoral glands of *Aotus* [Aquino & Encarnación, 1986].

### Trees Containing Holes

Nest holes were found in 67 old and senescent trees comprising 13 species. Among these, we found 40.2% of the sleeping sites in trunks and branches of *Eschweilera* sp., 12.0% in *Macrolobium acaciaefolium*, 10.3% in *Campsiandra laurifolia*, and 9.0% in *Calycophyllum spruceanum* (Table I). These tree species characteristically show disintegration of the heartwood even though the trunk, supported only by sapwood, remains erect and partially vegetative.

### Distribution of Sleeping Sites With Respect to Forest Strata

The ages of individual trees and their densities and crown shapes were factors that determined the location and selection of sleeping sites. In interpreting the location of these sites, the following forest strata were identified: understory (7.1–10.0 m), lower story (10.1–19.0 m), middle story (19.1–25.0 m), upper story (25.1–31.0 m), and emergent trees (31.1–37.0 m).

In the forest of the Tahuayo River, 21.4% of the sleeping sites of *Aotus nancymai* were in the shrub stratum of the understory, 64.3% were in the lower story, and 14.3% were in the middle story. No sleeping sites were found in the upper story or in emergent trees.

In contrast, in the forest of the Nanay and Napo Rivers, 11.4% of the sleeping sites of *A. vociferans* were in the understory, 54.3% were in the lower story, 20.0% were in the middle story, 8.6% were in the upper story, and 5.7% were in emergent trees (Table II; Fig. 3).

Each forest stratum had different forms of sleeping sites. The Aa, Da, and Db forms were found in the understory; the Ab, Ac, Ba, and Bb forms were found in the lower story; and the Ad, Ae, Ca, and Cb forms were frequently seen in the highest strata (Figs. 2 and 3).

### Competition Over and Sharing of the Sleeping Sites With Other Mammals

In *Aotus nancymai* and *A. vociferans*, we observed competition over and sharing of the type A sleeping sites with other mammals of similar nesting habits. The size and depth of the holes were important in these interactions. We observed one case

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Fig. 2. Types and forms of sleeping sites. A. Sleeping sites in holes. Aa. Apical position in palm trunk. Ab. Apical position in dicotyledonous tree trunk. Ac. Subaxial position. Ad. Subapical position. Ae. Lateral position. B. Complex sleeping sites in concavities with climbers and vines. Ba. Axial concavity. Bb. Subaxial concavity. C. Complex sleeping sites with hemiepiphytes and epiphytes. Ca. Subaxial position. Cb. Subapical position. D. Simple sleeping sites in thickets and dense foliage. Da. Axial position. Db. Irregular position.

TABLE I. Trees With *Actus* Nest Holes Observed in Amazon Lowlands of Peru

Species	Vernacular names	Frequency	Percentage
<i>Guilielma gasipaes</i>	Pijuayo	3	4.5
<i>Calycophyllum spruceanum</i>	Capirona	6	9.0
<i>Campsiandra laurifolia</i>	Huacapurana	7	10.3
<i>Clarisia biflora</i>	Capinuri	2	3.0
<i>Coccoloba</i> sp.	Vino Huayo	1	1.5
<i>Couroupita subsessilis</i>	Ayahuma	2	3.0
<i>Eschweilera</i> sp.	Machimango	27	40.2
<i>Ficus</i> sp.	Renaco	2	3.0
<i>Hura crepitans</i>	Catahua	2	3.0
<i>Iriarte</i> sp.	Huacrapona	3	4.5
<i>Macrolobium acaciaefolium</i>	Pashaco negro	8	12.0
<i>Manilkara</i> sp.	Quinilla	1	1.5
<i>Mauritia flexuosa</i>	Aguaje	3	4.5
Totals		67	100.0

of competition and six cases of co-occupation in several circumstances and localities. Moreover, bats often roosted in these cavities.

In the locality of Mishana on the Nanay River, for a family group of *Aotus vociferans* with three individuals we found four sleeping sites, one of which was used for 3 consecutive days. At 0525 hours on the 4th day, an adult *Potos flavus* entered the hole; 17 minutes later the *Aotus* group arrived but, hearing growls from within the cavity, did not enter and moved to another sleeping tree located 30 m away. After that incident, the *Aotus* group used two other sleeping trees for their diurnal rest, without returning to the first, even after it was abandoned by the *P. flavus*, which used it during 4 consecutive days.

Of the six cases of cohabitating, two were with *Potos flavus*, one was with *Bassaricyon gabbi*, and three were with *Coendu bicolor*. *Aotus* always occupied that part of the cavity nearest the entrance, while the interior-most part was occupied by the other species. All these co-occupants entered the sleeping sites between 15 to 20 minutes before *Aotus* and left between 20 and 25 minutes after *Aotus*.

These results indicate that competition occurred when the sleeping site was small and shallow and had only one entrance; co-occupation occurred when the sleeping site was large and deep and had two or more entrances, and where root mats of hemiepiphytes and hemiparasites formed lattice works used as substrata by the occupants.

TABLE II. Frequency Distribution of the Sleeping Sites by Forest Strata

Stratum	Height (m)	<i>A. nancymai</i>		<i>A. vociferans</i>	
		Frequency	Percentage	Frequency	Percentage
Understory	7.1–10.0	7	21.4	4	11.4
Lower story	10.1–19.0	27	64.3	19	54.3
Middle story	19.1–25.0	6	14.3	7	20.0
Upper story	25.1–31.0	0	0.0	3	8.6
Emergent trees	31.1–37.0	0	0.0	2	5.7
Totals		42	100.0	35	100.0

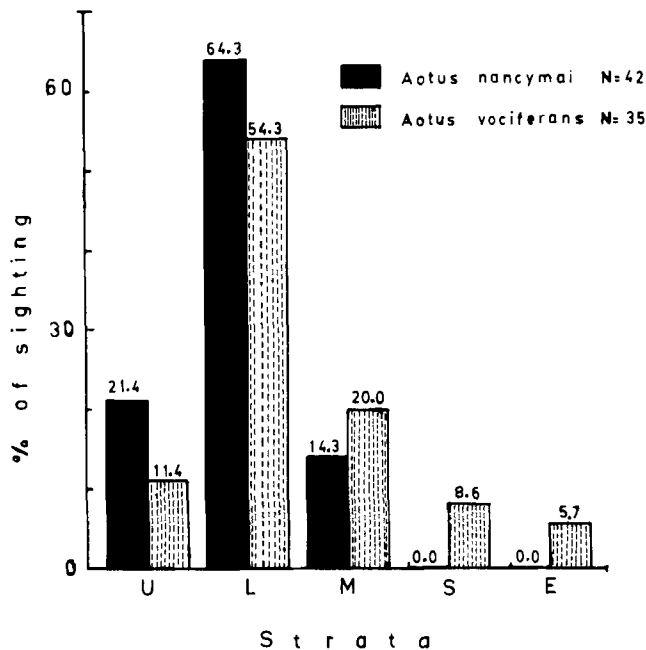


Fig. 3. Percentage distribution of *Aotus nancymai* and *A. vociferans* sleeping sites by forest strata. U, understory; L, lower story; M, middle story; S, upper story; E, emergent trees.

## DISCUSSION

The principal factors affecting the selection of sleeping sites of family groups include the following: 1) Protection and refuge from predators; 2) easy, routine, or circumstantial access; 3) shelter from weather conditions; and 4) sufficient space.

### Protection and Refuge From Predators

The intrinsic security of a sleeping site is assured by its position, location, and its provision for escape when predator attack so requires. These in turn require 1) isolation of the lodging tree, 2) optimum visibility in all directions, and 3) easy access and exit routes permitting rapid displacement when necessary. Isolation is achieved by surrounding water bodies such as lakes, rivers, streams, and swamps, which serve as barriers. For example, at the locality of Bombonaje on the Amazonas River, in a *Mauritia* palm swamp or "aguajal," the sleeping site of a family group with six members including an infant was found in the dry trunk of an isolated *Mauritia flexuosa* surrounded by open swamp with a few dispersed trees. The only access route to the lodging tree was via a large leaf of *Euterpe precatoria* palm.

### Easy, Routine, or Circumstantial Access

Lodging trees are generally mature, senescent, or lifeless and desintegrating trees. When sleeping sites are located on isolated trunks, the diameter usually does not exceed 30 cm, thereby facilitating vertical locomotion by short hops. When trunk diameter is greater than 30 cm, access is facilitated by climbers and vines hanging from the tree or by proximity of trees with thin trunks that lead directly or indirectly to the sleeping site.

### Shelter From Rain, Wind, and Abrupt Drops of Temperature

Shelter is afforded by nearly total protection from direct rainfall and by water running down leaves and branches. Sleeping sites in holes of senescent or dry trunks offer optimal conditions by virtue of the subapical, subaxial, and lateral position of the openings (see Fig. 2). In sleeping sites positioned at the bifurcation of principal branches, among vines, climbers, and epiphytes, or in thickets, protection from running water is afforded by 1) accumulations of disintegrating organic remains, which fill the interstices and form an impermeable cover at contact points or nodes in the vegetation, and 2) the laminar superposition of foliage, which facilitates runoff of water laterally. This protection from rainwear has the simultaneous benefit of providing protection from wind and of adequate temperature maintenance.

### Sufficient Space to Accomodate the Family Group

When sleeping sites are located in holes, the entrance is of variable dimensions between 14 and 35 cm, permitting the simultaneous entry of two or occasionally more individuals. The internal cavity can accomodate up to five individuals or, in exceptional circumstances, up to six. If the cavity is spacious and ample, simultaneous occupancy with other arboreal and nocturnal mammals can occur.

The 77 sleeping sites of *Aotus nancymai*, *A. vociferans*, and *Aotus* sp. [new karyotype, Ma et al, 1985] were grouped into four main types with all variant forms. The following three types coincide with those already described by other authors: a) tree holes [Thorington et al, 1976; Rathbun et al, 1980; Wright, 1981; Hershkovitz, 1983]; b) dense tangles of climbers and vines [Thorington et al, 1976; Wright, 1978, 1981; Rathbun et al, 1980; Hershkovitz, 1983]; and c) bamboos and dense thickets [Wright, 1981]. The fourth type described here occurs in concavities between the branches of trees, many are protected by dense entanglements of climbers, vines, root mats, and foliage of hemiepiphytes.

*Aotus nancymai* was found in all variants of all four types of sleeping sites, while *A. vociferans* was found only in tree holes of type A, coincident with the information of Hershkovitz [1983] that the "grey neck" *Aotus* of northern Colombia is found only in tree holes. This peculiarity of *A. vociferans* suggests the existence of a certain selectivity of habitat and occupation area and also might explain the absence or low population densities of *A. vociferans* in hillside forest (Aquino, unpublished data), where hardwood tree species predominate and trees with suitable nesting holes are rare.

Table II summarizes the observed variation in the position of sleeping sites with respect to height within the forest; *Aotus nancymai* appeared to prefer sites lower than 19.0 m, while *Aotus vociferans* often occupied also the middle and upper stories including emergents. Forest physiognomy, degree of disturbance, topography, and drainage are factors that may influence the selection of sleeping sites by *Aotus* species. These observed differences in habitat preferences and behavior by species of *Aotus* in the natural environment should be studied in more detail.

### CONCLUSIONS

1. Four types of sleeping sites were found with 11 different variant forms. *Aotus nancymai* was found in all forms of sleeping sites while *A. vociferans* was found only in the five forms of type A sleeping sites. None of these sleeping sites showed signs of nest-building.

2. Sleeping sites of *Aotus* offer protection, refuge, ease of routine, and circumstantial entry and exit, shelter, and sufficient space to lodge the family group.

3. *A. nancymai* sleeping sites were located in the under, lower, and middle stories of the forest below 25 m elevation, whereas *A. vociferans* slept also in the

upper and emergent stories up to 37 m elevation. On the average, *A. vociferans* tended to use higher sleeping sites than *A. nancymai*.

4. Competitive interactions and cohabitation of sleeping sites between *Aotus* and other nocturnal mammals were common.

5. The principal sapwood-bearing trees that presented holes for *Aotus* sleeping sites were *Eschweilera* sp. (40.2%), *Macrolobium acaciaefolium* (12.0%), *Campsian-dra laurifolia* (10.0%), and *Calycophyllum spruceanum* (9.0%).

## ACKNOWLEDGMENTS

We wish to thank the Comité Regional de Coordinación del Proyecto Primates No-Humanos in Iquitos for the facilities granted. We give special thanks to the guides and field workers, Mr. Desiderio Marichi, Juan Tapullima, and Gilberto Asipali for their efforts during predawn diurnal, crepuscular, and nocturnal labors in the Amazon forest. We also wish to thank Richard Madden for the English translation of the original manuscript and Dr. Kenneth Glander and Mr. Pekka Soini for their help with English phrasing. This work was performed as part of the activities of the Centro de Reproducción y Conservación de Primates No-Humanos of Iquitos, and was financed by the Proyecto Primates AMRO 3171, Peru, of the OMS/OPS.

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