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Roosting Ecology of Amazonian Bats: Evidence for Guild Structure in Hyperdiverse Mammalian Communities

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ABSTRACT

The ecological mechanisms that sustain high species richness in Neotropical bat communities have attracted research attention for several decades. Although many ecologists have studied the feeding behavior and diets of Neotropical bats on the assumption that food is a limiting resource, other resource axes that might be important for species coexistence are often ignored. Diurnal refugia, in particular, are a crucial resource for bats, many of which exhibit conspicuous morphological or behavioral adaptations to the roost environment. Here we report and analyze information about roost occupancy based on >500 field observations of Amazonian bats. Statistical analyses of these data suggest the existence of distinct groups of species roosting (1) in foliage, (2) exposed on the trunks of standing trees, (3) in cavities in standing trees, (4) in or under fallen trees, (5) beneath undercut earth banks, and (6) in arboreal insect nests; additionally, we recognize other groups that roost (7) in animal burrows, and (8) in rocks or caves. Roosting-guild membership is hypothesized to have a filtering effect on Amazonian bat community composition because some types of roosts are absent or uncommon in certain habitats. Among other applications of our results, cross-classifying bat species by trophic and roosting guilds suggests that the often-reported deficit of gleaning animalivores in secondary vegetation by comparison with primary forest might reflect habitat differences in roost availability rather than food resources. In general, ecological and evolutionary studies of Neotropical bats would be enhanced by considering both trophic- and roosting-guild membership in future analyses, but additional fieldwork will be required to determine the roosting behavior of many data-deficient species.

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Kuesban utsi-utsiek ikek. Kuesban kuëte tëdion uzhek. Kuesban mani padan uzhek. Kuesban meçhodon uzhek. Kuesban tazhodo tëdion uzhek. Kuesban kuëte tanunkiokkid dadiadek. Kuesban kuëtedapa tëdion kodotanaknombo kuesban utsi ikkid. Padnubi zhëkuëdapambik utsi tëmpadapa zhëkuëdapan. Kuesban dadpenkiozhë ikek. (Bats exist in different ways. Bats sleep under trees. Bats sleep in wild banana plants. Bats sleep in termite nests. Bats sleep under buttress roots. Bats hang on the trunks of very dry trees. Other bats are under big fallen trees, where the tree is twisted. Also, others are in big hollows, in big hollows of big *tëmpa* trees. There are very, very many kinds of bats.)

—Antonio Manquid Jiménez Tajur[4]

INTRODUCTION

Amazonian bats comprise some of the most diverse terrestrial vertebrate communities in the world. Estimates based on geographic range overlap (Voss and Emmons, 1996) predict that over 90 species might be sympatric everywhere in the region, and statistical extrapolations from local faunal-sampling results support similar conclusions (Simmons and Voss, 1998; Rex et al., 2008). Although numbers of sympatric bat species actually recorded in the course of Amazonian fieldwork are consistently fewer than those predicted by geographic range overlap or statistical extrapolations, they are still impressive. Lim and Engstrom (2001) reported 86 species from the Iwokrama Forest of central Guyana, Simmons and Voss (1998) found 78 species within a 3 km radius of their study site in northern French Guiana, and Sampaio et al. (2003) reported 72 species from an inventory project near Manaus in Brazil. Over 60 species have been reported from faunal survey efforts at several other Amazonian localities (Ascorra et al., 1993; Solari et al., 1999; Reid et al., 2000; Hice et al., 2004).

The ecological mechanisms that sustain high diversity in Neotropical bat communities have attracted research attention for several decades. Many zoologists assume—explicitly or implicitly—that trophic-resource partitioning is important for species coexistence, and this conviction has motivated a still-burgeoning literature on Neotropical bat diets and feeding behavior (e.g., Heithaus et al., 1975; Fleming et al., 1977; Bonaccorso, 1979; Bonaccorso and Gush, 1987; Thies et al., 1998; Dumont, 1999; Wendeln et al., 2000; Tschapka, 2004; Giannini and Kalko, 2004, 2005; Rex et al., 2011; Andrade et al., 2013; Saldaña-Vázquez, 2014). Various trophic-guild classifications have been defined on the basis of this research (LaVal and Fitch, 1977; Bonaccorso, 1979; Kalko et al., 1996), and trophic-guild membership is often used to assess Amazonian bat community structure (e.g., by Kalko and Handley, 2001; Lim and Engstrom, 2001; Bernard, 2002; Sampaio et al., 2003; Peters et al., 2006; Willig et al., 2007; Rex et al., 2008; Klingbeil and Willig, 2009; Bobrowiec and Gribel, 2010). However, food is not the only resource that might be limiting for bat populations, so community-ecological studies based exclusively on trophic categories could be misleading or incomplete.

[4] Part of an interview recorded in the Matses language at Nuevo San Juan, Loreto, Peru, on 1 July 1998 (see Fleck et al., 2002).

Diurnal refugia, in particular, are a crucial resource for bats, which spend at least half of their lives in the roost environment (Kunz, 1982). The autecological importance of bat roosts is suggested by numerous morphological and behavioral adaptations associated with roost occupancy in a wide range of species (Kunz, 1982; Thewissen and Etnier, 1995; Kunz and Lumsden, 2003; Dechmann et al., 2009; Santana et al., 2011), by the substantial energetic investment made by species that construct their own shelters (Dechmann et al., 2005; Rodríguez-Herrera et al., 2011), and by male defense of roosts in harem-forming species (Bradbury and Emmons, 1974; Morrison, 1979; Morrison and Morrison, 1981; Kunz and McCracken, 1996). Although some structures used as diurnal refugia—such as tree cavities and foliage—are seemingly abundant in many habitats, careful study of roost characteristics suggest that bats are highly selective about where they roost (Kunz and Lumsden, 2003), so ideal refugia may often be in short supply. The prompt colonization of artificial roosts deployed in experimental studies (e.g., Kelm et al., 2008) and the frequent use of manmade structures (buildings, bridges, culverts, etc.) as roosts support similar conclusions. That roosting behavior has been shaped by resource competition is suggested by consistent differences in this trait among closely related sympatric species (e.g., Bradbury and Emmons, 1974; Bradbury and Vehrencamp, 1976; Simmons et al., 2002; Bonaccorso et al., 2006; Velazco et al., 2014), a pattern not unlike the interspecific trophic differences that have long fascinated tropical bat researchers.

Because of its exceptional diversity, the Amazonian bat fauna provides a unique context within which to study the roosting habits of large numbers of sympatric species. Additionally, because much of the region remains undeveloped, community patterns of roost occupancy can still be observed in landscapes with minimal anthropogenic impact. By contrast, manmade structures that are often used as roosts by bats (e.g., buildings, bridges, and culverts) are ubiquitous in many other Neotropical biomes, perhaps obscuring aspects of chiropteran community structure that might otherwise be determined by natural-roost availability. Unfortunately, vast Amazonian landscapes are now being transformed by highway construction, agroindustry, logging, mining, and colonization, so a review of currently available information seems timely.

Here we report the results of a two-year survey of bat roosting behavior in northeastern Peru, where we enlisted the assistance of indigenous Amazonian hunters to obtain an unprecedented number of taxonomically vouchered roost observations. We combine these data with previously published reports of roosting behavior by Amazonian bats, resulting in an aggregate dataset of >500 observations. Statistical analyses of this dataset, the first to quantify the similarity structure of roost-occupancy data for any bat fauna, provide the basis for a guild classification that can be used in future studies of Amazonian bat community structure. We discuss the application of Root's (1967) guild concept to our results, discuss the extent to which roost availability might determine bat community structure in a variety of natural and anthropogenic Amazonian landscapes, and suggest how evolutionary scenarios previously interpreted in terms of trophic adaptations might usefully be supplemented by taking roosting-guild membership into account.

METHODS

Sources of roost data: We collected data on roost occupancy in 1998 and 1999 at Nuevo San Juan (5°15′S, 73°10′W; ca. 150 m above sea level), a Matses Indian village on the right bank of the Río Gálvez (a left-bank tributary of the Río Yavarí) in Loreto department, northeastern Peru (fig. 1: locality 27). Local habitats at this site (described by Fleck and Harder, 2000) include various edaphic formations of primary lowland rainforest as well as secondary growth resulting from swidden ("slash-and-burn") agriculture. In 1998 R.S.V. searched for roosts using procedures described by Simmons and Voss (1998: 17–19). Briefly, this involved deliberate visual searches of all likely roosting sites along trails (e.g., between buttresses of large standing trees, dark cavities under fallen trees, inside hollow logs, inside hollow standing trees, and among the foliage of large monocots). Roost observations (physical characteristics; species of sheltering plant, if known; number, sex, and provisional identification of resident bats) were recorded in a field journal and cross-referenced to a catalog of preserved voucher specimens (for relevant examples of journal and catalog entries, see Simmons and Voss, 2009: figs. 42.2, 42.4). In addition, R.S.V. was led to several roosts by Matses children and hunters, who found them in the course of play or subsistence activities in both primary forest and secondary vegetation.

In 1999 D.W.F. employed several Matses hunters from Nuevo San Juan to search for roosts. For the first several weeks of this field season D.W.F. accompanied Matses employees to each discovered roost site, where he recorded roost characteristics and collected voucher specimens. Later, after the Matses had been trained to record data and collect specimens themselves, small teams of Indians were encouraged to work independently. All of our Matses employees recorded their roost observations in the Matses language, which is rich in zoological, botanical, and habitat terminology (Fleck and Harder, 2000). Matses-authored roost observations (recorded in waterproof notebooks; see Fleck et al., 2002: fig. 2) were translated by D.W.F. soon after voucher specimens were preserved and recorded in archival documents as described above. Over the course of the 1999 field season, D.W.F. had numerous opportunities to visit roosts described in Matses field notes and found the latter to provide consistently accurate descriptions. Specimens collected as vouchers for roost observations at Nuevo San Juan were subsequently identified at the American Museum of Natural History (AMNH) by N.B.S. and P.M.V. The original field journals and specimen catalogs from this project are permanently archived at the AMNH (in New York), and duplicate sets of voucher specimens are preserved at the AMNH and at the Museo de Historia Natural de la Universidad Nacional Mayor de San Marcos (in Lima).

We additionally compiled records of roost occupancy from the literature (to the end of 2015), including taxonomic monographs, faunal inventory reports, and behavioral studies. Most of our tabulated records are based on vouchered taxonomic identifications (documented by cataloged specimens in museum collections), but we accepted unvouchered identifications of species with nonproblematic field characters (e.g., *Rhynchonyteris naso*, *Saccopteryx bilineata*, *Thyroptera tricolor*; Emmons, 1997), and we accepted unvouchered identifications of other species made by investigators with appropriate taxonomic expertise (e.g., Timm, 1987; Kalko et al., 2006). Such precautions are necessary because many Neotropical bat taxa (e.g., *Carollia*, *Artibeus*, glossophagines, molossids) include superficially similar species that are often difficult

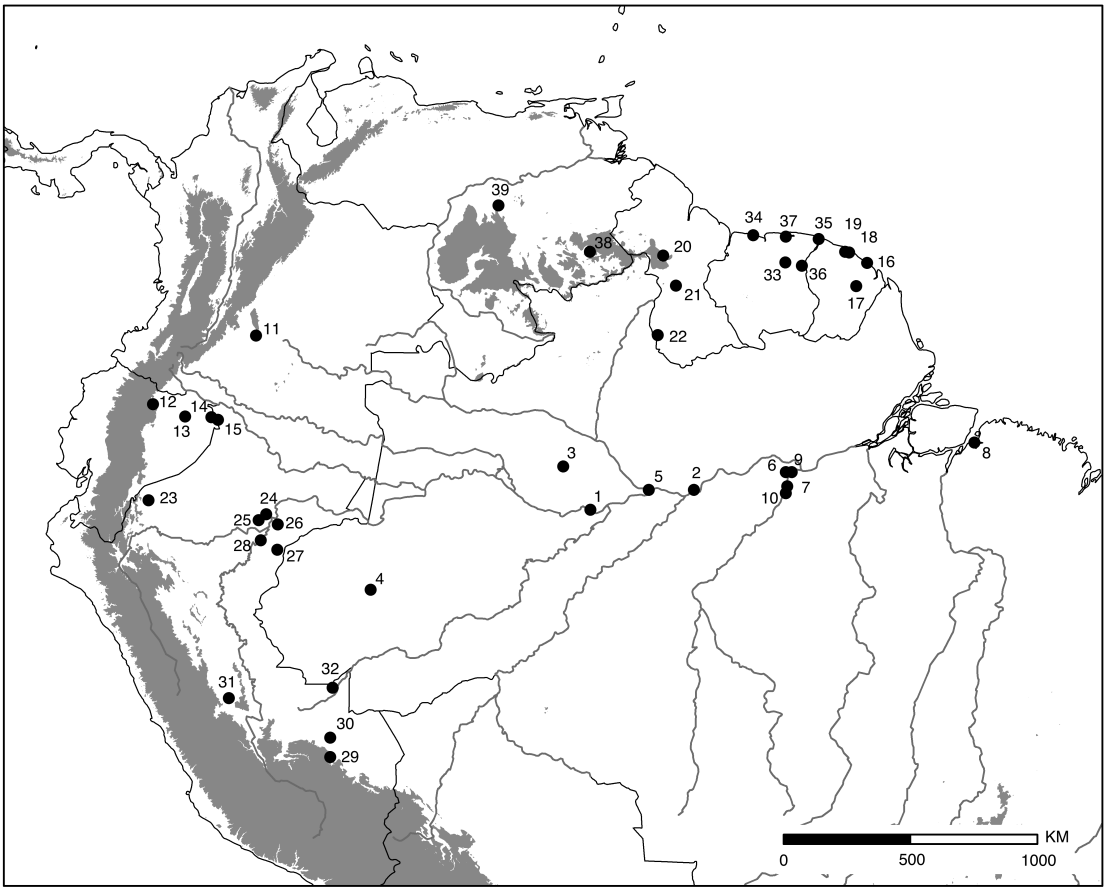

FIG. 1. Amazonian localities from which roost observations were compiled for this report. Numbers are keyed to gazetteer entries (appendix 1). Grayscale indicates elevations >1000 m above sea level.

to distinguish reliably in the field. When tabulating roost occupancy records from experimental studies of roosting behavior, we only included information from pretreatment observations; for example, we did not include observations of roosts that were used by bats after their natural refugia were experimentally destroyed (e.g., as by Charles-Dominique, 1993).

Insofar as possible we scored roost occupancy from primary accounts, not from subsequent compilations (e.g., field guides), and we did not score roost occupancy from any publication unless it was clear that a species had actually been found in a particular kind of roost. Therefore, statements that a species "roosts in foliage" (for example), without sufficient context to indicate that it was actually observed to do so by the authors, were ignored. We did not score information about roost occupancy from Linares (1998) because roost information in his book appears to be based on unattributed, previously published sources (e.g., Handley, 1979) rather than original observations. We were similarly unable to distinguish original roost observations in Graham (1988) from observations that he obtained from previous studies.

We encountered numerous ambiguities in published descriptions of roosting behavior, which we consistently interpreted as conservatively as possible. For example, a species said to

have been found "in hollow trees" during a particular study was interpreted to mean that it was found in a hollow tree at least once. Similarly, we did not score roost occupancy when descriptions were so vague (e.g., "roosts in trees") as to prevent definite assignment to one or another of our roost categories (see below).

Roost classification: We classified roosts by distinct physical characteristics and by the behavior of one or more species of bats that appear to use each roost type almost exclusively. For example, we recognize arboreal insect (termite and ant) nests as a distinct type of roost because they have unique physical features, and because species of *Lophostoma* are not known to roost elsewhere, despite the fact that termite nests are just one of several kinds of roosts used by *Phyllostomus hastatus*. However, we combined some roost types previously recognized by authors to facilitate tabulation if the information provided in the literature was routinely insufficient to distinguish them. For example, we combined unmodified leaves used as shelters by bats together with several kinds of modified-leaf shelters ("tents"; e.g., as described by Timm, 1987) into a single category ("foliage") because many published observations in the older literature did not allow us to make relevant distinctions. The distinction between rocks and caves used as shelters by bats was similarly problematic. Because our interest is in evolved roosting behavior, we did not tabulate roosts discovered in manmade structures. A few hard-to-classify roosts were assigned their own category ("other"), which was not treated in subsequent statistical analyses.

Animal burrow or hole (ABH): any dark hole in the ground roofed by soil and roots, including burrows excavated by animals and subterranean cavities of possibly erosional origin (Díaz and Linares-García, 2012: fig. 2E).

Cavity in fallen tree (CFT): any interior space in a toppled tree, typically the rotted-out central cavity of a hollow log (Simmons and Voss, 1998: figs. 27, 52).

Cavity in standing tree (CST): any interior space in a standing tree (alive or dead), often the rotted-out central core of the trunk, but also less extensive cavities made by animals (such as woodpeckers) and smaller cavities in the branches or roots caused by mechanical damage and subsequent decay (Simmons and Voss, 1998: figs, 21, 25, 26, 29).

Exposed on standing tree (EST): Any exposed surface on the trunk or branches of a standing tree, including shaded recesses flanked by buttresses (Bradbury and Emmons, 1974: fig. 2; Simmons and Voss, 1998: fig. 23).

Foliage (FOL): any leaf or leaves, alive or dead, usually of a palm or giant herb, but sometimes also of hemiepiphytes or dicotyledenous trees. Included in this category are unmodified leaves (Simmons and Voss, 1998: fig 15, 53, 54; Velazco et al., 2014: fig. 8) as well as those modified by bats as "tents" (Timm, 1987; Kunz et al., 1994).

Rocks and/or caves (R/C): any dark space sheltered by stony surfaces, such as crevices among piled boulders on talus slopes, cracks and fissures in large rocks exposed in riverbeds, or caverns eroded in the bedrock of cliffs or hillsides.

Termite/ant nest (TAN): any cavity excavated in the fabric of an arboreal termite or ant colony (Dechmann et al., 2004: fig. 1; York et al., 2008: fig. 1).

Under fallen tree (UFT): any dark recess under a partially or completely toppled tree (not including the hollow, tunnellike interior, if any); for example, on the undersides of buttresses, which are typically elevated a meter or more above the ground (Simmons and Voss, 1998: fig. 17), but also on the rounded underside of the trunk itself, especially when a tree has fallen across a stream or narrow ravine (Simmons and Voss, 1998: fig. 14).

Undercut earth bank (UEB): any open but shaded recess roofed by roots and soil along the margins of a stream, river, lake, or gully.

Taxonomy: Neotropical bat nomenclature has undergone extensive revision in just the last few decades, with the result that taxonomic usage in the older literature often differs from current usage. Several widely used epithets are no longer recognized as valid, some widespread "species" are now recognized as species complexes, and a few genera as formerly understood (e.g., *Lonchophylla*, *Tonatia*, *Mimon*) are now known to be paraphyletic. Taxonomic usage in this report follows Gardner (2008), who provided full bibliographic information (authors, dates, synonymies) for all binomina used herein, with the following exceptions: (1) we use *Gardnerycteris* as the appropriate genus for the bat formerly known as *Mimon crenulatum* after Hurtado and Pacheco (2014); (2) we use *Hsunycteris* for the species formerly known as *Lonchophylla thomasi* following Parlos et al. (2014), who also described the species *H. pattoni*; (3) our use of binomina in *Platyrrhinus* follows Velazco et al. (2010), who recognized *P. incarum* as a distinct species from *P. helleri* and described additional new species; and (4) we use *Micronycteris homezorum* as the appropriate spelling for *M.* "*homezi*" following Solari (2008). Additionally, we recognize that the bats currently known as *Sturnira lilium* represent a species complex that includes a distinct but still unnamed endemic Amazonian taxon (Velazco and Patterson, 2013).

Statistical analysis: To assess the extent to which Amazonian bats form distinct groups of species with similar roosting habits, we analyzed a dataset consisting of 34 species with five or more roost observations each. To estimate similarities in habitat use among pairs of species, we used Pianka's (1973) symmetric index of resource overlap between species j and k, $O_{jk} = O_{kj} = (\Sigma p_{ij} p_{ik})(\Sigma p_{ij}^2 \Sigma p_{ik}^2)^{-1/2}$, where p_{ij} is the proportion of roosts of species j belonging to roost category i, and the summations are over the previously defined roost categories (i = 1–9). This index is normalized to take on values between 0 (no resource overlap) and 1 (complete resource overlap). It has good statistical properties, and is stable under randomization (Gotelli and Graves, 1996). The complement of Pianka's index ($1 - O_{jk}$) was used as a measure of pairwise distance among species for subsequent analyses.

To assess the interspecific associations implied by these distance data, we used cluster analysis as implemented by the unweighted pair-group method with arithmetic averages (UPGMA; Sneath and Sokal, 1973), and we bootstrapped this analysis to estimate support statistics for recovered clusters of species (Strauss, 1982; Jaksič and Medel, 1990). The original data matrix was bootstrapped by repeatedly resampling the original frequency data with replacement, recalculating the distance matrix and dendrogram topologies, and keeping track of the frequency of occurrence of unique clusters.

An alternative way to display the information contained in a distance matrix is by multidimensional scaling (MDS; Shepard, 1962). Multidimensional scaling is a nonhierarchical ordination method that attempts to reproduce pairwise distances with minimal distortion by assigning coordinates to each point (species) in an *N*-dimensional geometric space. The more dimensions used, the better the fit of the original distances by the distances among points in the new coordinate space. Two commonly used measures of goodness of fit are the cophenetic correlation (the Pearson correlation between the original and coordinate distances) and "stress" (a residual sum of squares). Because we subsequently used species coordinates from MDS as input for a metric classification procedure (see below), we used metric MDS fitting rather than the more familiar nonmetric MDS. For metric MDS, the cophenetic correlation and stress are perfectly negatively correlated, so only the cophenetic correlation was calculated. To estimate the minimum number of dimensions needed to adequately reproduce the original distance matrix, we varied *N* from 1 to 6 and evaluated the corresponding cophenetic correlations.

To estimate the number and compositions of groups of species in the MDS coordinate space, we used a "k nearest-neighbor" (kNN) classification procedure (Strauss, 2001). We modified the nearest-neighbor algorithm described by Knorr et al. (2000) to identify and omit outliers from the recognized groups based on k rather than all nearest neighbors.

All statistical analyses were performed using Matlab v7.10 (Strauss, 2012).

RESULTS

We recorded 169 occupied roosts sheltering 41 species of bats at Nuevo San Juan from 1998 to 1999 (appendix 2). The commonest types of roosts encountered at this locality were cavities in standing trees (22% of all recorded roosts), foliage (20%), cavities in fallen trees (19%), the undersides of fallen trees (14%), the exposed surfaces of standing trees (7%), animal burrows (7%), and undercut earth banks (6%). Additionally, a few roosts were found in termite nests and in "other" (difficult to categorize) situations. Most roosts were found at ground level or within a few meters of the ground—an inevitable consequence of ground-based visual searching—but some trees were climbed and others were felled to search for roosts in subcanopy woodpecker holes.

Unfortunately, these data are too few to infer the preferred roost types of more than a handful of species. We recorded only one roost each for nine species, only two roosts each for six more species, and only three roosts each for another six species. In effect, over 60% of the species for which roosting data are available from this locality are represented by fewer than five observations. However, many commonly observed species (with ≥5 roost records) clearly preferred just one type of roost: under fallen trees (e.g., *Cormura brevirostris*), inside cavities in fallen trees (*Furipterus horrens*, *Micronycteris microtis*), inside cavities in standing trees (*Carollia perspicillata*, *Molossus rufus*, *Phyllostomus elongatus*, *Phyllostomus hastatus*), exposed on standing trees (*Saccopteryx leptura*), and in foliage (*Artibeus anderseni*, *Mesophylla macconnelli*, *Thyroptera tricolor*).

Such results suggest that modal patterns of roost use could be determined for many more bats if it were possible to accumulate enough observations. We therefore combined our roost-occupancy data from Nuevo San Juan with previously published observations to obtain a total of 585 roost observations for 83 species of bats from 39 research sites across the length and breadth of Amazonia (table 1, fig. 1). Visual inspection of this larger dataset supports some inferences about modal roosting behavior inferred from the Nuevo San Juan results and suggests that additional species also have strong predilections for particular kinds of roosts: in foliage (e.g., *Artibeus gnomus*, *A. planirostris*, *Rhinophylla pumilio*, *Uroderma bilobatum*), in cavities in standing trees (*Noctilio albiventris*, *Gardnerycteris crenulatum*, *Micronycteris hirsuta*), in cavities in fallen trees (*Hsunycteris thomasi*, *Micronycteris microtis*), exposed on standing trees (*Rhynchonycteris naso*), under fallen trees (*Choeroniscus minor*), inside arboreal termite nests (*Lophostoma silvicolum*), and beneath undercut earth banks (*Carollia castanea*).

Cluster analysis applied to the distance matrix computed from a subset of these frequency data (comprising 34 species with ≥5 observations; see Methods) suggests the existence of several statistically robust groups of species with similar roosting habits (fig. 2). In order of distinctness, the first of such clusters (Group I) consists of bats that roost exclusively, or almost exclusively, in foliage (*Artibeus anderseni*, *A. glaucus*, *A. gnomus*, *A. planirostris*, *Mesophylla macconnelli*, *Rhinophylla pumilio*, *Uroderma bilobatum*, *Thyroptera tricolor*, *Eumops auripendulus*). The next best-supported cluster (Group II) includes two species that roost almost exclusively on the exposed surfaces of tree trunks (*Rhynchonycteris naso*, *Saccopteryx leptura*). A more numerous but less strongly supported cluster (Group III) includes some bats that roost primarily inside cavities of standing trees (*Saccopteryx bilineata*, *Noctilio albiventris*, *Carollia perspicillata*, *Gardnerycteris crenulatum*, *Micronycteris hirsuta*, *Phyllostomus elongatus*, *P. hastatus*, *Trachops cirrhosus*, *Molossus rufus*), but the last few species that join this group (*Carollia brevicauda*, *Glossophaga soricina*, *Micronycteris megalotis*) often use other refugia. Group IV includes species that usually roost in or under fallen trees, but which sometimes use other dark ground-level refugia (*Cormura brevirostris*, *Peropteryx kappleri*, *P. leucoptera*, *P. macrotis*, *P. pallidoptera*, *Choeroniscus minor*, *Hsunycteris thomasi*, *Micronycteris microtis*, *Furipterus horrens*). There are, additionally, two unaffiliated "groups" in these results, one consisting of a species that only roosts beneath undercut earth banks (*Carollia castanea*) and another that roosts exclusively in termite nests (*Lophostoma silvicolum*).

The results of metric multidimensional scaling suggest that three coordinate axes provide a reasonably good fit (cophenetic correlation = 0.78) to the distance matrix. All of the four groups identified by UPGMA clustering form nonoverlapping polygons on two-dimensional projections of the MDS coordinate space (not shown), and the same groups are recovered by our kNN classification procedure with the two unaffiliated species identified as outliers. Thus, the group structure in our data seems to be recoverable by both hierarchical and nonhierarchical procedures.

TABLE 1. Frequencies of roost occupancy by Amazonian bats.

		Roost types[a]										
	N[b]	ABH	CFT	CST	EST	FOL	R/C	TAN	UFT	UEB	other	Source(s)[c]
EMBALLONURIDAE												
Centronycteris maximiliani	2			1		1						1, 36
Cormura brevirostris	23		2	4	1	1			15			1–5
Diclidurus scutatus	1					1						4
Peropteryx kappleri	13		5				1		7			1–3
Peropteryx leucoptera	14	1	5			1			7			1, 2, 5–8
Peropteryx macrotis	6		1	1			1		2	1		1, 3, 4, 8
Peropteryx pallidoptera	13	3	1			1			5	3		2, 5
Rhynchonycteris naso	9				9							2–5, 9, 10
Saccopteryx bilineata	31		3	17	9				1		1	1–6, 8, 9–11
Saccopteryx canescens	1						1					4
Saccopteryx leptura	14			1	9	2					2	1–3
PHYLLOSTOMIDAE												
Ametrida centurio	2					2						10, 35
Anoura caudifer	3		1							2		2, 10, 13
Anoura geoffroyi	1						1					4
Artibeus (D.) anderseni	10					10						2, 5, 14
Artibeus (D.) cinereus	1					1						1
Artibeus (D.) glaucus	5					5						2, 14
Artibeus (D.) gnomus	15					15						1, 14, 15
Artibeus (A.) lituratus	4					4						1, 2, 10, 16
Artibeus (A.) obscurus	6			1	1	1					3	1, 2, 10
Artibeus (A.) planirostris	5					5						5, 17
Carollia brevicauda	20	3	8	7					1	1		2, 5, 8, 18
Carollia castanea	11									11		19
Carollia perspicillata	36	2	5	27					1	1		1–3, 5, 8, 10, 18, 19
Choeroniscus minor	8					1			6	1		1, 2, 8, 10, 20
Desmodus rotundus	1			1								10
Gardnerycteris crenulatum	5			5								5, 11, 18
Glossophaga soricina	9		4	4						1		1, 2, 4, 5, 10
Glyphonycteris daviesi	3			3								2, 3, 21
Glyphonycteris sylvestris	2			2								2, 22

		Roost types[a]										
	N[b]	ABH	CFT	CST	EST	FOL	R/C	TAN	UFT	UEB	other	Source(s)[c]
Hsunycteris pattoni	4		4									2
Hsunycteris thomasi	12		8						3	1		1, 2, 5, 12, 16
Hsunycteris sp. nov.	2									2		2
Lampronycteris brachyotis	2			2								2
Lionycteris spurrelli	1						1					4
Lonchorhina aurita	1			1								10
Lonchorhina inusitata	1						1					4
Lophostoma brasiliense	2							2				2, 23
Lophostoma carrikeri	1							1				24
Lophostoma silvicolum	14							14				2, 5, 8, 23
Macrophyllum macrophyllum	3		1				1			1		2, 4, 10
Mesophylla macconnelli	20					20						1, 2, 8, 25
Micronycteris brosseti	1			1								1
Micronycteris hirsuta	6	1		5								1–3
Micronycteris homezorum	1			1								2
Micronycteris matses	4	4										2
Micronycteris megalotis	14		4	6				1	2	1		1–5, 8–10
Micronycteris microtis	19	5	11	3								1, 2
Micronycteris minuta	1			1								8
Mimon bennettii	2			1			1					1, 4
Phyllostomus elongatus	11			10						1		1–3, 5, 26
Phyllostomus hastatus	17			9		1	1	6				2, 3, 5, 6, 9–11
Phyllostomus latifolius	1						1					4
Platyrrhinus fusciventris	2					2						16, 35
Platyrrhinus incarum	1					1						27
Platyrrhinus infuscus	3						1			2		2, 3
Rhinophylla pumilio	65					65						1, 2, 15, 28
Tonatia saurophila	2			2								11, 18
Trachops cirrhosus	5		2	3								2, 10, 18
Uroderma bilobatum	6					6						1, 10, 16
Uroderma magnirostrum	1					1						14
MORMOOPIDAE												
Pteronotus parnellii	1						1					4
NOCTILIONIDAE												
Noctilio albiventris	9			9								4, 9, 10, 12

		Roost types[a]										
	N^b	ABH	CFT	CST	EST	FOL	R/C	TAN	UFT	UEB	other	Source(s)[c]
Noctilio leporinus	1			1								10
FURIPTERIDAE												
Furipterus horrens	20		6	2					11	1		1, 2, 8
THYROPTERIDAE												
Thyroptera discifera	2					2						10, 34
Thyroptera lavali	1					1						29
Thyroptera tricolor	22					22						1, 2, 4, 8–10
Thyroptera wynneae	1					1						30
MOLOSSIDAE												
Cynomops abrasus	1					1						9
Eumops auripendulus	5			1		4						10
Eumops glaucinus	1			1								10
Eumops trumbulli	1					1						9
Molossus molossus	2			2								10
Molossus rufus	6			6								2, 10
Nyctinomops laticaudatus	2						2					4, 31
VESPERTILIONIDAE												
Eptesicus brasiliensis	2										2	2, 32
Lasiurus blossevillii	1					1						16
Lasiurus ega	1					1						10
Myotis albescens	3		1	1							1	2, 10
Myotis nigricans	2					1	1					4, 9
Myotis riparius	1										1	33
Myotis simus	2			1		1						10
Totals	585	19	72	142	29	183	15	24	61	30	10	

[a] Abbreviated as described in text.

[b] Number of roost observations.

[c] Sources: 1, Simmons and Voss (1998); 2, this study; 3, Tuttle (1970); 4, Brosset and Charles-Dominique (1990); 5, Díaz and Linares-García (2012); 6, Ascorra et al. (1993); 7, Bernard (1999); 8, Rengifo et al. (2013); 9, Reis and Peracchi (1987); 10, Patterson (1992); 11, Hice et al. (2004); 12, Barnett et al. (2006); 13, Griffiths and Gardner (2008); 14, Timm (1987); 15, Charles-Dominique (1993); 16, Husson (1978); 17, Jimbo and Schwassmann (1967); 18, Bernard and Fenton (2003); 19, Bonaccorso et al. (2006); 20, Sanborn (1954); 21, Solari et al. (1999); 22, Williams and Genoways (1980); 23, Kalko et al. (2006); 24, Allen (1911); 25, Foster (1992); 26, Shapley et al. (2005); 27, Tello and Velazco (2003); 28, Henry and Kalko (2007); 29, Gregorin et al. (2006); 30, Velazco et al. (2014); 31, Barriga-Bonilla (1965); 32, Divoll et al. (2015); 33, Lim et al. (1999); 34, Torres et al., 1988; 35, Charles-Dominique and Brosset (2001); 36, Rocha et al. (2015).

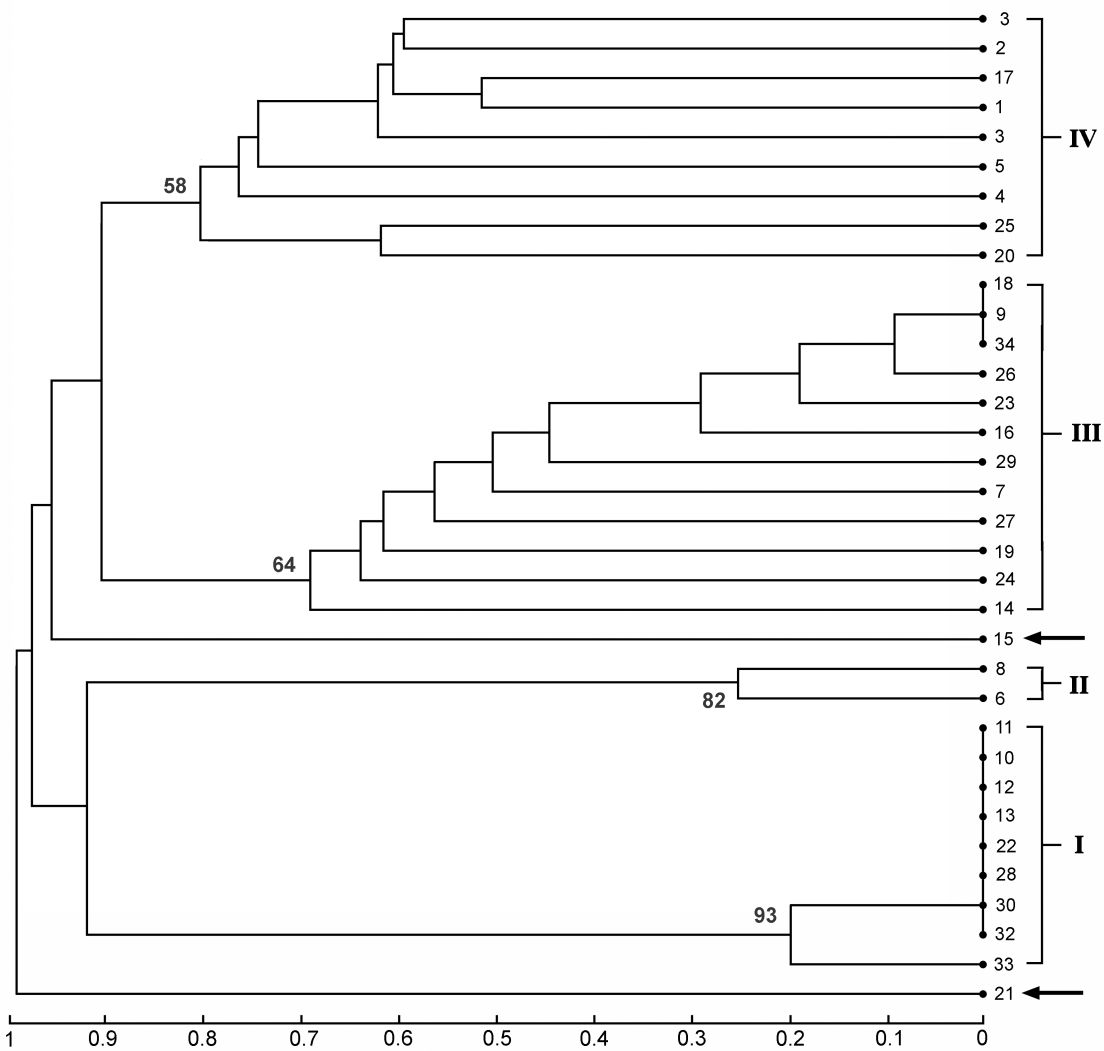

FIG. 2. UPGMA dendrogram of 34 Amazonian bat species clustered by roosting-niche distance (see text). Numbers adjacent to internal nodes are bootstrap percentages, Roman numerals indicate multispecies groups discussed in the text, and arrows indicate unaffiliated species. Key to terminal taxa: **1,** *Cormura brevirostris*; **2,** *Peropteryx kappleri*; **3,** *P. leucoptera*; **4,** *P. macrotis*; **5,** *P. pallidoptera*; **6,** *Rhynchonycteris naso*; **7,** *Saccopteryx bilineata*; **8,** *S. leptura*; **9,** *Noctilio albiventris*; **10,** *Artibeus anderseni*; **11,** *A. glaucus*; **12,** *A. gnomus*; **13,** *A. planirostris*; **14,** *Carollia brevicauda*; **15,** *C. castanea*; **16,** *C. perspicillata*; **17,** *Choeroniscus minor*; **18,** *Gardnerycteris crenulatum*; **19,** *Glossophaga soricina*; **20,** *Hsunycteris thomasi*; **21,** *Lophostoma silvicolum*; **22,** *Mesophylla macconnelli*; **23,** *Micronycteris hirsuta*; **24,** *M. megalotis*; **25,** *M. microtis*; **26,** *Phyllostomus elongatus*; **27,** *P. hastatus*; **28,** *Rhinophylla pumilio*; **29,** *Trachops cirrhosus*; **30,** *Uroderma bilobatum*; **31,** *Furipterus horrens*; **32,** *Thyroptera tricolor*; **33,** *Eumops auripendulus*; **34,** *Molossus rufus*.

ROOSTING GUILDS OF AMAZONIAN BATS

The most striking pattern in the data compiled for this study is that most Amazonian bats for which relevant data are available seem to be roost specialists. With few exceptions, each species with multiple roost observations is commonly found in only one or two of the nine categories of daytime refugia defined above. Additionally, although many species are sometimes found in atypical roosts, our statistical analyses suggest that more or less distinct groups of species with similar roosting habits can be identified.

Following standard ecological usage (Root, 1967; Pianka, 1980; Jaksič, 1981; Simberloff and Dayan, 1991; Blondel, 2003), we define a guild as a group of species that exploit the same class of environmental resources in a similar way.[5] Foliage, for example, can be considered a class of environmental resources that various bat species use in a similar way (for diurnal shelter), so it seems appropriate to recognize a guild of foliage-roosting species. Note that guilds (1) are not equivalent to niches, which correspond to the unique sets of resources required by individual species; (2) do not necessarily correspond to groups of species that compete for the same resource, although they may often do so; and (3) are not defined by taxonomy, and so do not necessarily include closely related species (Root, 1967; Jaksič, 1981; Simberloff and Dayan, 1991).

Below we provide a roosting-guild classification of Amazonian bats based on the results summarized above supplemented by observations from extralimital studies (appendix 3). The latter often corroborate Amazonian patterns of roost occupancy (*Lophostoma silvicolum*, for example, seems to roost in termite nests wherever it is found), but extralimital observations suggest that behavioral shifts sometimes occur where other roosting opportunities exist. Caves and rocks, for example, are absent from much of Amazonia. Bats that often roost in caves in Central America (e.g., *Desmodus rotundus*) cannot be widely distributed in Amazonian habitats (as they frequently are) unless they also use other kinds of roosts, so it is reasonable to classify a species that roosts in both caves and tree cavities in Central America but has only been taken in tree cavities in Amazonia as a member of the tree-cavity-roosting guild in the latter biome. Implicit in this logic is the possibility that the same species may belong to different guilds in different regions.

Although uncommon in the context of this study, generalist species—species that use a wide range of resources—are problematic for any meaningful guild classification (Simberloff and Dayan, 1991). Trophic generalists, for example, are sometimes placed in an "omnivore" guild, but this practice would seem to be inconsistent with the definition of a guild, because no particular class of resources is uniquely exploited by its members. We address this ambiguity by simply identifying roost generalists as such, leaving them unassigned to guild.

Lastly, despite efforts to objectify the recognition of guilds (e.g., by Jaksič and Medel, 1990), the exercise seems irremediably subjective in many respects, beginning with what constitutes a "class" of environmental resources and how similar species must be in their use of those

[5] Some bat researchers (e.g., Rex et al., 2008) use "ensemble" (sensu Fauth et al., 1996) as a synonym for "guild." However, like Stroud et al. (2015), we prefer the more familiar term, which has been used by animal ecologists for many years with minimal confusion. "Functional group" is another term that is sometimes used as a synonym for "guild", but we agree with Blondel (2003) that guilds and functional groups are distinct ecological concepts.

TABLE 2. Suggested roosting-guild classification of Amazonian bats.[a]

I. Species that roost in foliage *Cyttarops alecto*, *Diclidurus albus*, *D. scutatus*, *Ametrida centurio*(?), *Artibeus (A.) lituratus*, *A. (A.) planirostris*, *A. (D.) anderseni, A. (D.) cinereus*, *A. (D.) glaucus*, *A. (D.) gnomus*, *Mesophylla macconnelli*, *Platyrrhinus fusciventris*, *P. incarum*, *Rhinophylla pumilio*, *Uroderma bilobatum*, *U. magnirostrum*, *Vampyrodes caraccioli*, *Thyroptera discifera*, *T. lavali*, *T. tricolor*, *T. wynneae*, *Eumops auripendulus*(?), *Promops centralis*(?), *Lasiurus blossevillii*, *L. ega*
II. Species that roost in exposed situations on standing trees: *Rhynchonycteris naso*, *Saccopteryx canescens*, *S. leptura*
III. Species that roost in cavities in standing trees *Saccopteryx bilineata*(?), *Carollia perspicillata*, *Chrotopterus auritus*, *Desmodus rotundus*, *Gardnerycteris crenulatum*, *Glyphonycteris daviesi*, *G. silvestris*, *Lampronycteris brachyotis*, *Micronycteris hirsuta*, *M. minuta*, *M. schmidtorum*, *Mimon bennettii*, *Phyllostomus discolor*, *P. elongatus*, *Phyllostomus hastatus*(?), *Tonatia saurophila*, *Trachops cirrhosus*(?), *Trinycteris nicefori*, *Vampyrum spectrum*, *Noctilio albiventris*, *N. leporinus*, *Cynomops planirostris*, *Eumops glaucinus*, *Molossus coibensis*, *M. molossus*, *M. rufus*, *Myotis nigricans*(?), *M. simus*.
IV. Species that roost in or under fallen trees *Cormura brevirostris*, *Peropteryx kappleri*, *P. leucoptera*, *P. macrotis*(?), *P. pallidoptera*(?), *Choeroniscus minor*, *Hsunycteris pattoni*, *H. thomasi*, *Micronycteris microtis*, *Furipterus horrens*
V. Species that roost under earth banks *Anoura caudifer*(?), *Carollia castanea*, *Hsunycteris* sp. nov., *Platyrrhinus infuscus*(?)
VI. Species that roost in arboreal insect nests *Lophostoma brasiliense*, *L. carrikeri*, *L. silvicolum*
VII. Species that roost in animal burrows *Micronycteris matses*
VIII. Species that roost in rocks or caves *Anoura geoffroyi*, *Diphylla ecaudata*, *Lionycteris spurrelli*, *Lonchorhina aurita*, *L. inusitata*, *Phyllostomus latifolius*, *Pteronotus gymnonotus*, *P. parnellii*, *P. personatus*, *Natalus tumidirostris*, *Neoplatymops mattogrossensis*, *Nyctinomops laticaudatus*
Species with generalized roosting habits (not assigned to guilds) *Carollia brevicauda*, *Glossophaga soricina*, *Micronycteris megalotis*

[a] See text for assignment criteria, and note that many Amazonian taxa remain unclassified to guild because information about their roosting behavior is unavailable.

resources to justify grouping them together (Root, 1967; Simberloff and Dayan, 1991). We acknowledge this subjectivity as well as the inadequacy of quantitative analyses to do much more than graphically depict resource-use similarities among the better-sampled species in this study. Therefore, we provide brief discussions of the criteria we used to include or exclude species from each guild whenever guild membership departs from the results of our analyses.

Guild I. Species that roost in foliage: The extraordinary diversity of leaf morphologies, crown architectures, and stem heights among Neotropical rainforest plants, especially monocots (trees, treelets, giant understory herbs, hemiepiphytes, etc.), offers a corresponding host of structurally distinct shelters for foliage-roosting bats from ground level to the canopy.[6] Whereas the physical properties of leaves determine the number and size of bats that can roost in foliage of a particular plant species, as well as how such leaves can be modified by their inhabitants to provide suitable diurnal refugia (Kunz et al., 1994), leaf phenology determines how often resident bats must seek new shelters (e.g., Vonhof and Fenton, 2004). Bats roosting

[6] See Cooley et al. (2004) and Grubb and Jackson (2007) for examples of the various anatomical, physiological, and adaptive trade-offs that result in leaves with different roosting opportunities for bats.

in foliage near ground level are probably vulnerable to different sets of predators than are bats roosting in canopy foliage, perhaps resulting in additional adaptations correlated with stem height. All of these factors suggest that it may often be advantageous for foliage-inhabiting bats to be specialized in their roosting habits.

The foliage roosts of many taxa referred to this guild are reasonably well documented by published Amazonian records (*Artibeus anderseni*, *A. glaucus*, *A. gnomus*, *A. planirostris*, *Mesophylla macconnelli*, *Rhinophylla pumilio*, *Uroderma bilobatum*, *Thyroptera tricolor*; table 1) and/or by extra-Amazonian observations (e.g., *Cyttarops alecto*, *Diclidurus albus*, *A. cinereus*, *A. lituratus*; appendix 3). Most of these species are not known to use any other kind of roost, and foliage-roosting species form a correspondingly well-defined cluster in our statistical analyses (fig. 2). However, we are uncertain about the assignment of *Eumops auripendulus* to this guild, because other congeneric species use different kinds of roosts, and because the species itself does not exhibit any obvious morphological adaptations to foliage roosting. Additionally, all of the records of this species roosting in foliage are from a single source, which might be biased for a number of reasons.

We assigned other species to this guild if (1) the species in question is definitely known to roost in foliage, (2) the species exhibits morphological traits consistent with this behavior (see below), and (3) closely related species also roost in foliage. Thus, although some species of thyropterids are known from just one or two roost observations, all exhibit adaptations for foliage roosting (adhesive suckers on the wrist and ankle; Kunz, 1982; Kunz and Lumsden, 2003), and no congener has ever been found in any other kind of natural roost. The same logic suggests that *Diclidurus scutatus*, *Vampyrodes caraccioli*, *Lasiurus blossevillii*, and *L. ega* also belong here. *Ametrida centurio* and *Promops centralis* are more hypothetical assignments.

Members of this guild differ in how they use foliage as diurnal refugia. Many foliage-roosting phyllostomids construct tentlike shelters by deliberately modifying the large leaves of various monocot species, whereas foliage-roosting emballonurids, thyropterids, and vespertilionids occupy unmodified leaves or clusters of leaves.[7] Such divergent habits might justify the recognition of tent-making bats on the one hand and bats that use unmodified foliage on the other as different guilds (or subguilds) in future refinements of our classification, but other distinctions might be equally relevant for community-ecological studies. For example, some foliage-roosting species occupy understory vegetation (e.g., *Mesophylla macconnelli*, *Thyroptera tricolor*), whereas others are thought to occupy the canopy or subcanopy (e.g., *Artibeus lituratus*, *Vampyrodes caraccioli*), and this behavioral difference may have some significance for bat assemblages in unflooded versus seasonally inundated forests (see below). For the time being, therefore, a broadly defined guild of foliage-roosting taxa seems least problematic.

Other Amazonian bat species almost certainly belong to this guild, but relevant behavioral data are equivocal or entirely lacking. As several authors have noted, bright facial stripes and pale (white or whitish) coloration are correlated with leaf-roosting habits (Kunz, 1982; Kunz and

[7] This seemingly clear distinction is somewhat blurred by one phyllostomid species (*Rhinophylla pumilio*), which sometimes occupies unmodified foliage but also uses leaf tents that are probably constructed by stenodermatines (Charles-Dominique, 1993; Zortéa, 1995; Simmons and Voss, 1998).

Lumsden, 2003; Santana et al., 2011), and the Amazonian fauna includes many species with such traits, all or most of which might roost in leaves. Among other candidate taxa are species of *Vampyressa* and *Vampyriscus*, but none of the Amazonian members of these genera are definitely known to roost in foliage. Several species of *Platyrrhinus* might also roost in foliage, but *P. fusciventris* and *P. incarum* seem to be the only Amazonian species definitely known to do so.

Guild II. Species that roost on exposed surfaces of standing trees: Tree trunks are ubiquitous in Amazonian habitats, but most do not seem to provide suitable surface roosts for bats. Careful studies of bats belonging to this guild suggest that they favor shallow concavities or other situations that provide some protection from the elements, and trees with deeply corrugated or flaking bark seem to be avoided (Bradbury and Emmons, 1974). In our experience, roosts on exposed tree trunks are also quite free of encroaching foliage.

The two Amazonian species definitely assigned to this guild—*Saccopteryx leptura* and *Rhynchonycteris naso*, both emballonurids—form one of the best-defined clusters in our statistical analyses. We tentatively also assign *S. canescens* to this group based on multiple roost observations from the Venezuelan Llanos (Ibáñez, 1981), despite the fact that the only observed Amazonian roost was in rocks (Brosset and Charles-Dominique, 1990). Other species of *Saccopteryx* might also belong here, but Amazonian roosts of *S. bilineata* have been found almost twice as often in cavities of standing trees as they have been on exposed trunks, and this species clusters with members of Guild III in our statistical analyses. The roosting habits of *S. gymnura*, another Amazonian congener, are unknown.

Guild III. Species that roost in cavities in standing trees: Standing trees with rotted-out central cavities are abundant in Neotropical rainforests—about a third of large trees in central Amazonia have hollow cores (Apolinário and Martius, 2004)—so it is not surprising that numerous species of bats use such cavities as diurnal roosts. Many trees with hollow cores have openings at or near ground level, and these are the shelters in which bats are most commonly found by visual searching. Additionally, the upper trunk and branches of standing trees are often drilled by woodpeckers or have holes caused by mechanical damage and subsequent decay (Boyle et al., 2008), and such cavities are also occupied by bats. These two kinds of cavities are perhaps used by different sets of species, but we lack enough well-documented observations to assert this as a fact. The ornithological literature (e.g., Brightsmith, 2005) suggests that tree cavities are visited by predators (snakes, opossums) that might prey on resident bats, but information is lacking on this point, nor is it known whether predation risk differs with cavity size, type, or height above the ground.

Membership in this guild is reasonably well documented by Amazonian observations for five species that apparently use cavities in standing trees almost exclusively in the absence of caves (*Gardnerycteris crenulatum*, *Micronycteris hirsuta*, *Phyllostomus elongatus*, *Noctilio albiventris*, *Molossus rufus*); a sixth species (*Carollia perspicillata*) is much more frequently found in tree cavities than in other kinds of natural Amazonian roosts, although it often inhabits manmade structures (especially culverts) where these are available. Three other species that cluster with these six in our statistical analyses (*Saccopteryx bilineata*, *Phyllostomus hastatus*, *Trachops cirrhosus*) are tentatively included here; tree cavities represent >50% of their reported

roosts, but each also often occurs elsewhere (*S. bilineata* on the exposed trunks of standing trees, *P. hastatus* in termite nests, and *T. cirrhosus* in hollow logs). Three additional species that are the last to join this cluster and may account for its relatively weak bootstrap support appear to be generalists with no clearly distinguishable modal roosting behavior (*Carollia brevicauda*, *Glossophaga soricina*, *Micronycteris megalotis*).

We assign another 19 species to this guild based on the preponderance of evidence from both Amazonian and extralimital observations (table 1, appendix 3). Known natural roosts of these species are exclusively in tree cavities (*Glyphonycteris daviesi*, *G. sylvestris*, *Lampronycteris brachyotis*, *Micronycteris schmidtorum*, *Tonatia saurophila*, *Trinycteris nicefori*, *Vampyrum spectrum*, *Cynomops planirostris*, *Eumops glaucinus*, *Molossus coibensis*, *M. molossus*, *M. pretiosus*, *Myotis simus*) or in tree cavities and caves (*Chrotopterus auritus*, *Desmodus rotundus*, *Micronycteris minuta*, *Mimon bennettii*, *Phyllostomus discolor*, *Noctilio leporinus*). In central Amazonia, where caves and rocks are largely absent, the latter species are presumably found almost exclusively in tree cavities, but along the base of the Andes or in other areas with rock outcrops these taxa might as appropriately be referred to Guild VIII (see below).

Guild IV. Species that roost in or under fallen trees: Although treefalls are frequent events in Neotropical lowland rain forests (Chambers et al. [2000] suggest seven treefalls per hectare per year as an average rate for central Amazonian forests), there appear to be no relevant studies of the density of prostrate tree trunks, nor of their important characteristics as animal refugia. Amazonian bats find diurnal shelter on the undersides of large fallen trees, often between buttresses at the base of uprooted trunks, which form dark, concave recesses that may be elevated a meter or more above the ground. However, bats also roost on the rounded (convex) undersides of smooth, unbuttressed trunks that have fallen across streams or gullies, especially when these are clear of entangling vegetation. Logs with rotted-out central cavities provide additional roosting opportunities for bats that use such tunnellike structures, which sometimes have multiple openings.

A reasonably well-defined group of Amazonian species is primarily associated with fallen trees, although some guild members are also found occasionally in other ground-level shelters (e.g., animal burrows or undercut earth banks). Two species in this guild (*Cormura brevirostris* and *Choeroniscus minor*) seem to strongly prefer roosts on the undersides of fallen trees, whereas three others (*Micronycteris microtis*, *Hsunycteris pattoni*, *H. thomasi*) are more frequently found inside hollow logs. Several species, however, are found with almost equal frequency in both situations (e.g., *Peropteryx kappleri*, *P. leucoptera*, *Furipterus horrens*), which inclines us to consider fallen trees as a single resource class. We are not confident about the guild membership of *Peropteryx macrotis* and *P. pallidoptera*, which seem to be somewhat generalized in their use of ground-level refugia. Several members of this Amazonian guild are often found in caves or rocks elsewhere in the Neotropics (appendix 3).

Guild V. Species that roost beneath undercut earth banks: River banks, stream banks, lake shores, and the sides of headwater gullies in hilly terrain are often undercut by water action or soil slippage in the rainy season, resulting in dark, cavelike recesses roofed by soil and roots. Fifteen species of Amazonian bats have been found roosting in such places, at

least one of which—*Carollia castanea*, possibly a complex of morphologically similar taxa (Velazco, 2013)—seems to be a roost specialist. Although this guild is uniquely represented by *C. castanea* in our statistical results, at least three other species seem to belong here too. Two of the latter, *Anoura caudifer* and *Platyrrhinus infuscus*, are rock- and/or cave-roosting species elsewhere in their geographic distributions (Gardner, 2008), and the use of undercut earth banks as diurnal roosts plausibly explains their presence at several central Amazonian localities without rock outcrops. Undercut earth banks seem to have seldom been searched for bat roosts, and we predict that future attention to this distinctive roost category will result in many new and interesting observations, plausibly including new guild members.

Guild VI. Species that roost in arboreal insect nests: Arboreal termite nests (termitaria) and arboreal ant nests can be found from near ground level to the subcanopy in most Neotropical forests (e.g., Lubin et al., 1977). Both kinds of nests are known to provide diurnal shelters for birds (Brightsmith, 2000) as well as bats. Although several genera of termites construct arboreal nests, the largest nests—and the ones most commonly occupied by birds and bats—are constructed by species of *Nasutitermes* (Brightsmith, 2000; Kalko et al., 2006; York et al., 2008). Arboreal ant nests, which can also be quite large (to 2 m in length), are constructed by species of the genus *Azteca*. Statistical comparisons of termitaria occupied and unoccupied by bats suggest that bats prefer large, active, well-shaded termite nests that are freely accessible from below (Kalko et al., 2006), but the salient characteristics of ant nests occupied by bats have not been investigated.

Amazonian members of this roosting guild include three species of *Lophostoma*, of which *L. silvicolum* is definitely known to excavate its own roosting cavities in termitaria (rather than occupying cavities made by birds, as was once believed; Kalko et al., 2006). Apparently, *L. brasiliense* and *L. silvicolum* are only known to occupy termitaria, but the Central American species *L. kalkoae* was found roosting in a hollowed-out *Azteca* ant nest (Velazco and Gardner, 2012), and the unique roost description of the closely related (and morphologically similar) Amazonian species *L. carrikeri* suggests that it too might have been taken in an ant nest rather than a termitarium.[8] The large omnivorous bat *Phyllostomus hastatus* has sometimes been found roosting in termitaria, usually in the company of *L. silvicolum* (e.g., by Tuttle, 1970), but *P. hastatus* more frequently inhabits cavities in standing trees and statistically clusters with members of Guild II; it is not believed to excavate its own roosts in termite nests (Kalko et al., 2006).

Guild VII. Species that roost in animal burrows: Several Amazonian mammals, including armadillos (e.g., *Dasypus kappleri*) and pacas (*Cuniculus paca*), excavate deep burrows in the banks of streams or headwater gullies, and these tunnellike cavities are sometimes occupied by bats. Holes of possibly erosional origin are difficult to distinguish from long-abandoned burrows, and might shelter similar bat faunas.

[8] Allen (1911) quoted the collector (M.A. Carriker) as stating that specimens of *Lophostoma carrikeri* ". . . were all taken in a hollowed-out termite nest, hanging from a vine . . . When I passed under the nest one flew out, which gave me the clue, and I fired into the nest on suspicion, with the result that it rained bats for a moment." Despite the explicit statement that the roost was a termite nest, several aspects of this description—supported only by a vine, hollowed out, and unresistant to shotgun pellets—better fit the lighter fabric of an *Azteca* ant nest than the massive constructions of *Nasutitermes* spp.

Seven Amazonian bat species have been reported from animal burrows (or erosional holes), six of which are more commonly found in other kinds of shelters. However, animal burrows are the only known roost of *Micronycteris matses*, which was collected from burrows on multiple occasions at Nuevo San Juan by our Matses colleagues (who assiduously search stream banks and headwater gullies seeking *Dasypus kappleri*, a preferred game species; Fleck and Voss, 2016). We expect that searching animal burrows for roosting bats elsewhere in Amazonia may result in the discovery of other members of this somewhat hypothetical guild, which is not represented in our statistical analyses.

Guild VIII. Species that roost in rocks and/or caves: As noted earlier, rocky outcrops and caves are virtually absent from central Amazonia, although they are common along the base of the Andes and among the eroded quartzite and sandstone remnants of the Roraima Formation in southern Venezuela and the Guianas. There are, additionally, scattered granitic outcrops elsewhere in northeastern Amazonia (Gröger and Huber, 2007), and large fissured boulders are sometimes exposed along central Amazonian rivers and streams.

These geological features provide shelter for a number of bats that seem to use them almost exclusively. This is, perhaps, not properly an Amazonian guild, given that rocks and caves are uncommon in the region, but we list the species for which cave- and rock-roosting is best documented, principally in reports from extralimital studies (appendix 3).

DISCUSSION

Although the guild concept as originally proposed by Root (1967: 335) was defined in general terms ("a group of species that exploit the same class of environmental resources in a similar way"), the concept has usually been applied to trophic categories (Simberloff and Dayan, 1991). However, Root himself referred to nesting guilds (of birds), and subsequent researchers have validly applied the guild concept to a wide range of nontrophic resources (e.g., Schmidt and Whelan, 1998; Johnson and Romero, 2004; Potts et al., 2005). Indeed, we are not the first to recognize roosting guilds of bats, although neither of the publications known to us in which this phrase previously occurred (Findley, 1993; Flaquer et al., 2007) treated the concept in any depth.

Members of the same guild are commonly expected to compete with one another (Root, 1967; Blondel, 2003), but observing competition is not a practical criterion for inferring guild membership, nor should guild members be assumed a priori to interact competitively (Jaksič, 1981; Simberloff and Dayan, 1991). Although it seems plausible that the roosting-guild structure of Amazonian bat communities reflects structural differences among roost types ("natural gaps in resource space"; Pianka, 1980) that make it difficult for generalists to compete effectively with specialists, we have no hard evidence to support this conjecture. Many of the observed differences in roosting behavior among members of the same guild (e.g., those described by Bradbury and Emmons, 1974; Timm, 1987; Velazco et al., 2014) might be inherited traits that evolved in the context of past competitive interactions, such that guild members do not currently compete with one another for roost sites, but competitive interactions (past or present) are not a prerequisite for roosting-guild membership to affect the composition of bat communities.

Implications for Community Ecology

Although most ecological studies of Amazonian bat communities have focused on trophic-guild structure, some researchers have suggested that roosting behavior can affect community composition in both natural and anthropogenic habitats (Brosset et al., 1996; Kalko and Handley, 2001; Sampaio et al., 2003). Perhaps the most obvious consequence of roosting behavior for Amazonian bat ecology is the filtering effect it probably has on the entire regional fauna. Except along the base of the Andes, and in parts of the Guiana Region (as noted above) rocky outcrops are almost entirely absent from Amazonian landscapes, and the absence (or rarity) of several rock- and/or cave-roosting Neotropical clades—notably mormoopids and natalids—is one of the most distinctive characteristics of central Amazonian bat communities.

A similar filtering effect attributable to roosting behavior could be expected in Amazonian river floodplains, where members of Guilds IV (which primarily roost in or under fallen trees), V (which roost beneath undercut earth banks), and VII (which roost in animal burrows) should be largely absent from bat communities in extensive tracts of seasonally inundated forest (*várzea* and *igapó*; Prance, 1979). Foliage-roosting species (members of Guild I) that primarily inhabit understory vegetation might also be sparsely represented in flooded-forest communities by comparison with communities in upland forests. These expectations are partially corroborated by one recent survey of bat communities in flooded versus unflooded Amazonian forests (Pereira et al., 2009), which reported statistically significant differences in the relative abundances of *Carollia castanea*, *Mesophylla macconnelli*, and *Rhinophylla pumilio* that are plausibly explained by roosting behavior.[9] However, a subsequent study (Bobrowiec et al., 2014) reported seemingly contradictory results. Unfortunately, several members of Guild IV are seldom captured in mist nets even where these bats are known to be abundant (e.g., *Peropteryx leucoptera*, *Micronycteris microtis*, and *Furipterus horrens* at Paracou, French Guiana; Simmons and Voss, 1998: table 69), so testing this prediction with standard survey methods might be difficult. Future field research with the object of analyzing bat community differences in flooded versus unflooded Amazonian forests should supplement mist-netting with other methods (e.g., acoustic monitoring) to obtain more taxonomically comprehensive results.

A third example of the filtering effect that roosting behavior might have on bat community composition concerns members of Guild III (species that roost in tree cavities), which should be less abundant in extensive tracts of secondary vegetation (where large hollow trees are typically absent) than in primary forest (where such shelters are abundant).[10] Although bat community differences between primary forest and secondary growth have often been reported in the literature, the results are usually interpreted in terms of trophic-guild membership. In particular, secondary vegetation is consistently said to be deficient in gleaning-animalivorous species by comparison with primary forest (e.g., by LaVal and Fitch, 1977; Simmons and Voss,

[9] Foliage roosts of *Mesophylla macconnelli* and *Rhinophylla pumilio* are consistently found in understory vegetation (see references in table 1).

[10] This prediction should be tempered by the recognition that some members of Guild III (e.g., *Carollia perspicillata*) often roost in manmade structures (culverts, buildings, etc) that are almost always found in close proximity to secondary vegetation.

TABLE 3. Amazonian bat species cross classified by trophic- and roosting-guild membership.[a]

	Roosting Guilds							
Trophic Guilds	I	II	III	IV	V	VI	VII	VIII
Aerial insectivores	11	3	8	6				6
Gleaning animalivores			13	1		3	1	2
Piscivores			1					
Sanguivores			1					1
Frugivores	14		1		2			
Nectarivores				3	2			2

[a] Cell entries are numbers of species belonging to corresponding row classes (trophic guilds; based on the literature) and column classes (roosting guilds; from table 2). Feeding guilds are simplified from Sampaio et al. (2003) and incorporate the usual taxonomic assumptions (that trophically unstudied species of emballonurids, thyropterids, molossids, and vespertilionids are aerial insectivores; that unstudied glossophagines and lonchophyllines are nectarivores; etc.). Following Simberloff and Dayan (1991), we do not recognize "omnivory" (e.g., as exemplified by *Phyllostomus* spp.; Sampaio et al., 2003) as a valid dietary guild.

1998; Bobrowiec and Gribel, 2010; Farneda et al., 2015). Although we do not dispute this frequently reported result, we note that it is difficult to explain in trophic terms, because the large insects and small vertebrates that are preyed upon by gleaning-animalivorous bats seem to be abundant in secondary vegetation (LaVal and Fitch, 1977). However, cross-classifying bat species by trophic and roosting guilds (table 3) suggests an alternative explanation. Most gleaning-animalivorous bats for which roost information is available inhabit tree cavities, so the commonly observed trophic difference between bat communities in secondary vegetation and primary forest might reflect a habitat difference in roost availability rather than food resources.

Evolutionary Implications

Among the nine families that comprise the Amazonian bat fauna, Phyllostomidae has the widest representation among the guilds recognized in this report (table 4), suggesting an evolutionary diversification in roosting behavior that rivals the family's widely recognized disparity in trophic adaptations. Next in roosting-guild diversity, however, is Emballonuridae, a clade that consists exclusively of aerial insectivores. Although the diversity of roosting habits of molossids and vespertilionids is almost certainly underrepresented by these results (see below), the wide range of roosting behaviors among phyllostomids and emballonurids is striking and invites speculation about the role of roosting adaptations in the evolution of these groups.

Studies of phyllostomid adaptive radiation have hitherto focused exclusively on feeding behavior (e.g., Wetterer et al., 2000; Datzmann et al., 2010; Monteiro and Nogueira, 2011; Dumont et al., 2011; Rojas et al., 2011), resulting in scenarios that are sometimes accompanied by impressive analyses of trophic morphology. Although dietary adaptations have almost certainly played an important role in phyllostomid evolution, causal inferences in this literature would be strengthened if alternative behavioral traits that might also have influenced relevant evolutionary phenomena were considered. For example, recent phylogenetic studies (Dumont

TABLE 4. Higher-taxonomic representation in Amazonian roosting guilds.[a]

	Roosting Guilds							
	I	II	III	IV	V	VI	VII	VIII
Emballonuridae	3	3	1	5				
Phyllostomidae	14		18	4	4	3	1	6
Mormoopidae								3
Noctilionidae			2					
Furipteridae				1				
Thyropteridae	4							
Natalidae								1
Molossidae	2		5					2
Vespertilionidae	2		1					

[a] Table entries are numbers of species.

et al., 2011; Shi and Rabosky, 2015; Rojas et al., 2016) have detected a statistically significant diversification-rate shift at or near the base of the subfamily Stenodermatinae, a clade that comprises predominantly frugivorous species. Dumont et al. (2011) attributed this rate shift, which resulted in a marked increase in lineage accumulation, to the evolution of new cranial phenotypes that improved frugivorous-feeding performance. However, frugivory is not the only derived behavioral trait shared by stenodermatines, which also include almost all the phyllostomid species known to roost in foliage, as well as *all* the phyllostomid species believed to modify leaves as tentlike shelters. Because tent making, like frugivory, also involves biting through resistant plant tissues, it might be difficult to distinguish the morphological correlates of dietary versus roosting adaptations in this clade. Nevertheless, future analyses of phyllostomid adaptive radiation might usefully model both roosting behavior and feeding behavior as alternative (or joint) drivers of estimated diversification rates, although causal analyses of evolutionary rate shifts are likely to remain problematic (Rabosky and Goldberg, 2015).

Unlike phyllostomids, an endemic Neotropical clade, emballonurids also occur in the Paleotropics. According to the only published comparative analysis of emballonurid roosting behavior, the Old World taxa are said to occupy dark refugia (caves, rock crevices, tree cavities, hollow logs), whereas a greater diversity of roosts are apparently used by New World lineages. In Lim and Dunlop's (2008) parsimony optimization of roosting habits on emballonurid phylogeny, foliage roosting evolved once (on the branch subtending *Cyttarops alecto* + *Diclidurus* spp.), and roosting on exposed tree trunks also evolved once (on the branch subtending *Rhynchonycteris naso* + *Saccopteryx* spp.). Unfortunately, other categories of roosts occupied by New World emballonurids (e.g., under fallen trees, inside cavities of standing trees) were lumped together in their study, their scoring of terminal taxa does not agree in all cases with information compiled for this report, and they scored roosting habits for some species (e.g., *Diclidurus isabella*, *D. ingens*, *Saccopteryx gymnura*) that we have been unable to verify from published observations. Despite such reservations, Lim and Dunlop's results suggest that roosting behavior is conserved in some clades, especially when it is accompanied by other phenotypic adaptations (such as concealing coloration).

Conservation Implications

Large-scale anthropogenic conversion of Amazonian landscapes from primary forest to secondary growth seems likely to affect bat communities in ways that can be predicted, in part, by roosting-guild membership. As discussed above, members of Guild III (which roost in cavities in standing trees) are conspicuously underrepresented in secondary growth by comparison with primary forest, presumably due to the loss of old hollow trees by clear-cutting. Some members of Guild III (e.g., *Carollia perspicillata*) are well known to roost in culverts and other manmade refugia, but many others do not, including the majority of gleaning-animalivorous Amazonian bats. Among other consequences, the loss of gleaning animalivorous bats might have negative consequences for subsistence agriculture and forest regeneration, because these bats provide important ecosystem services by limiting insect herbivory (Kalka et al., 2008). Even more drastic landscape alterations, such as conversion to agroindustry will predictably result in the extirpation of most bat species that do not roost in manmade structures, although some foliage-roosting species are likely to persist in palm plantations.

Future Directions

Although bat biologists have long recognized the autecological importance of roosts (Kunz, 1982; Kunz and Lumsden, 2003), roosting behavior has seldom been analyzed in the context of community-ecological comparisons nor as an element of reconstructed adaptive scenarios. This is probably due to the fact that—unlike dietary habits—roost occupancy can seldom be inferred from morphology. Instead, roosting behavior must be observed in the field, and this is often hard to do. We are persuaded that incorporating roosting-guild membership in future analyses holds promise for more detailed and nuanced ecological and evolutionary understanding of the uniquely diverse Amazonian fauna, but future research with this objective will require accurate information about the roosting behavior of many more taxa.

Molossids and vespertilionids, in particular, are underrepresented in the data compiled for this report, as are several phyllostomid genera (e.g., *Chiroderma*, *Sturnira*, *Vampyriscus*) and numerous species, some of which are widespread (e.g., *Phylloderma stenops*, *Rhinophylla fischerae*, *Sphaeronycteris toxophyllum*, *Vampyressa thyone*). Because almost all of our data were obtained by ground-based visual searching, the most likely explanation for many of these data-deficient taxa is that they normally roost well above ground level, perhaps in subcanopy foliage or tree cavities. Future fieldwork to fill in these and other taxonomic gaps in our knowledge of Amazonian bat roosting behavior might profitably use radiotelemetry to locate the diurnal refugia of mist-netted individuals (Bernard and Fenton, 2003).

Plausible outcomes of future research include revisions or refinements of our guild classification as new data accumulate. The possibility of recognizing subguilds of foliage-roosting species has already been mentioned, but new guilds are another. For example, Amazonian bats have been found roosting under loose bark on standing trees (Simmons and Voss, 1998: fig. 40) and under loose bark on prostrate trees in gaps (appendix 2: Roost 4); both roosts were scored as "other" in this report for lack of sufficient evidence that either represents a distinct

roost category. Repeated observations like these might justify the recognition of novel roost categories, but new data could also suggest that our guild classification is oversplit (e.g., if it turns out that species roosting beneath undercut earth banks frequently also use animal burrows), or insufficiently resolved (e.g., if abandoned woodpecker holes are home to a bat fauna distinct from that of central cavities in standing trees). Like any other classification, ours will be tested and, inevitably, changed in light of new information.

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APPENDIX 1

Gazetteer of Amazonian Localities with Published Records of Bat Roosting Behavior

Below we list all of the Amazonian localities (or clusters of adjacent localities) associated with published descriptions of bat diurnal roosts. Geographic coordinates (in parentheses) are decimal degrees of latitude and longitude sufficient only for coarse mapping purposes (fig. 1). Cited sources are those from which roost observations were obtained, but coordinate data may have been obtained from other, uncited sources.

BRAZIL

1. *Amazonas,* Codajáz (-3.833, -62.083); Patterson (1992).
2. *Amazonas,* Itacoatiara (-3.133, -58.417) and adjacent localities Lago do Baptista and Lago Tapayuna; Patterson (1992).
3. *Amazonas,* Jaú National Park (ca. -2.300, -63.050); Barnett et al. (2006).
4. *Amazonas,* João Pessoa (-6.667, -69.867); Patterson (1992).
5. *Amazonas,* Manaus (-3.133, -60.017) and adjacent localities; Reis and Peracchi (1987)
6. *Pará,* Alter do Chão (-2.502, -54.955) and adjacent localities near Santarém, including Ilha de Urucurituba; Patterson (1992), Bernard (1999), Bernard and Fenton (2003).
7. *Pará,* Aveiros (-3.250, -55.167); Patterson (1992).
8. *Pará,* Belém (-1.450, -48.483); Jimbo and Schwassmann (1967).
9. *Pará,* Iroçanga (-2.500, -55.167); Patterson (1992).
10. *Pará,* Prainha (-3.000, -55.117); Patterson (1992).

COLOMBIA

11. *Meta,* La Angostura (2.333, -73.917); Barriga-Bonilla (1965).

ECUADOR

12. *Napo,* Cascada San Rafael (-0.0967, -77.5733); Timm (1987).
13. *Orellana,* Tiputini Biodiversity Station (-0.5333, -76.4333); Bonaccorso et al. (2006).
14. *Sucumbíos*, Lagarto Cocha (-0.5583, -75.5000); Timm (1987).
15. *Sucumbíos*, Zancudo Cocha (-0.6500, -75.2667); Timm (1987).

FRENCH GUIANA (FRANCE)

16. Montjoly (4.9000, -52.2833); Brosset and Charles-Dominique (1990).
17. Nouragues (4.0833, -52.6667); Brosset and Charles-Dominique (1990), Charles-Dominique (1993), Henry and Kalko (2007).
18. Paracou (5.2753, -52.9236); Simmons and Voss (1998).
19. Piste de St. Elie (5.3000, -53.0667); Brosset and Charles-Dominique (1990), Charles-Dominique (1993).

GUYANA

20. *Potaro-Siparuni,* Echerak (5.1667, -59.5000); Shapley et al. (2005).
21. *Potaro-Siparuni,* Surama Sawmill (4.1000, -59.0500); Lim et al. (1999).
22. *Upper Takutu-Upper Essequibo,* Tamton (2.350, -59.700); Gregorin et al. (2006).

PERU

23. *Amazonas,* Soledad (-3.5000, -77.7333); Solari et al. (1999).
24. *Loreto,* numerous localities along road from Iquitos to Nauta (ca. -3.9917, -73.5583); Hice et al. (2004), Díaz and Linares-García (2012).
25. *Loreto,* several localities near Seis Unidos (-4.2017, -73.8225); Rengifo et al. (2013).
26. *Loreto,* field station of German Primate Center (-4.3500, -73.1500); Kalko et al. (2006).
27. *Loreto,* Nuevo San Juan (-5.2500, -73.1667); this study.
28. *Loreto,* Jenaro Hererra (-4.9167, -73.7500); Ascorra et al. (1993), Velazco et al. (2014).
29. *Madre de Dios,* Cerro de Pantiacolla (-12.5833, -71.3000); Timm (1987).
30. *Madre de Dios,* Cocha Cashu Biological Station (-11.9000, -71.3000); Foster (1992), Tello and Velazco (2003), Divoll et al. (2015).
31. *Pasco,* San Juan (-10.5000, -74.88333); Tuttle (1970).
32. *Ucayali*, Balta (-10.1333, -71.2167); Griffiths and Gardner (2008).

SURINAM

33. *Brokopondo,* Brownsberg Nature Park (4.9167, -55.1833); Williams and Genoways (1980).
34. *Coronie,* Coronie (5.8833, -56.3167); Husson (1978).
35. *Marowijne,* Galibi (5.7500, -54.0000); Husson (1978).
36. *Marowijne,* Nassau Mountains (4.8000, -54.6000); Husson (1978).
37. *Paramaribo,* Paramaribo (5.8333, -55.1667); Husson (1962, 1978).

VENEZUELA

38. *Bolívar,* Chimantá-tepui (5.3000, -62.1000); Sanborn (1954).
39. *Bolívar,* Río Mocho (6.9500, -65.333); Allen (1911).

APPENDIX 2

Bat Roosts Discovered in 1998 and 1999 at Nuevo San Juan, Loreto, Peru

We numbered roosts sequentially at Nuevo San Juan in order of discovery, with a few inadvertently duplicated numbers distinguished subsequently by alphabetic suffixes. Roost types are abbreviated as explained in the text, but foliage roosts in leaf tents (LT) are distinguished from those in unmodified foliage (UF). Height is the estimated distance above ground level (in meters, m) of roosting groups of resident bats, but roosts discovered in holes in the ground, under earth banks, and those found in or under fallen trees were assigned a height of 0.0 m by convention; missing height data are indicated by an em-dash (—). Some roosts (marked with asterisks) were visited more than once; the names of bats observed on visits after the first are enclosed by parentheses.

Roost	Type	Height	Species
1	FOL (LT)	1.5	*Mesophylla macconnelli*
2	UFT	0.0	*Peropteryx pallidoptera, Saccopteryx bilineata*
3	TAN	2.0	*Lophostoma silvicolum*
4	other	0.0	*Eptesicus brasiliensis, Myotis albescens*
5	FOL (LT)	1.3	*Mesophylla macconnelli*
6	CFT	0.0	*Peropteryx pallidoptera*
7	TAN	1.6	*Lophostoma brasiliense*
8	other	2.0	*Saccopteryx leptura*
9	CFT	0.0	*Micronycteris microtis*
10	CFT	0.0	*Peropteryx kappleri*
11	CFT	1.5	*Cormura brevirostris*
12	FOL (LT)	1.3	*Mesophylla macconnelli*
13	FOL (UF)	2.0	*Artibeus glaucus*
14	UEB	0.0	*Furipterus horrens*
15	UEB	0.0	*Peropteryx pallidoptera*
16	FOL (UF)	1.8	*Artibeus glaucus*
17	FOL (LT)	1.2	*Mesophylla macconnelli*
18	UFT	0.0	*Cormura brevirostris*
19	UFT	0.0	*Furipterus horrens*
20	UFT	0.5	*Peropteryx pallidoptera*
21	CFT	0.0	*Micronycteris microtis, Carollia brevicauda*
22	UFT	0.0	*Peropteryx pallidoptera*
23	EST	5.0	*Saccopteryx bilineata*
24*	FOL (LT)	6.0	*Artibeus glaucus, (Rhinophylla pumilio)*
25a	FOL (LT)	1.0	*Mesophylla macconnelli*

Roost	Type	Height	Species
26a	FOL (UF)	6.0	*Saccopteryx leptura*
25b	CST	3.5	*Carollia perspicillata*
26b	FOL (LT)	1.0	*Mesophylla macconnelli*
27	UFT	0.0	*Cormura brevirostris*
28	UEB	0.0	*Hsunycteris* sp. nov.
29	FOL (LT)	1.0	*Mesophylla macconnelli*
30	FOL (LT)	2.0	*Rhinophylla pumilio*
31	ABH	0.0	*Peropteryx pallidoptera, Micronycteris matses, Carollia brevicauda*
32	UEB	0.0	*Platyrrhinus infuscus*
33	FOL (LT)	—	*Mesophylla macconnelli*
34	UFT	0.0	*Choeroniscus minor*
35	EST	4.0	*Cormura brevirostris*
36	CFT	0.0	*Furipterus horrens*
37	UFT	0.0	*Hsunycteris thomasi*
38	UFT	0.0	*Cormura brevirostris*
39	CFT	0.0	*Hsunycteris pattoni*
40	UFT	0.0	*Furipterus horrens*
41	CFT	0.0	*Micronycteris microtis*
42	TAN	4.0	*Phyllostomus hastatus, Lophostoma silvicolum*
43	UFT	0.0	*Macrophyllum macrophyllum*
44	FOL (LT)	1.0	*Mesophylla macconnelli*
45	CFT	0.0	*Micronycteris microtis*
46	CST	15.0	*Saccopteryx bilineata*
47	CST	10.0	*Carollia perspicillata*
48	CFT	0.0	*Peropteryx kappleri*
49	TAN	2.5	*Lophostoma silvicolum*
50a	CST	10.0	*Molossus rufus, Noctilio albiventris*
50b	CST	9.0	*Phyllostomus hastatus*
51	CST	9.0	*Molossus rufus*
52	CST	—	*Noctilio albiventris*
53	CFT	0.0	*Hsunycteris pattoni*
54	CFT	0.0	*Carollia brevicauda*
55	ABH	0.0	*Micronycteris matses*
56	FOL (UF)	1.0	*Peropteryx pallidoptera*
57	CST	3.0	*Carollia brevicauda, C. perspicillata*
58	UEB	0.0	*Glossophaga soricina*
59	CFT	0.0	*Micronycteris microtis*
60	CFT	0.0	*Furipterus horrens*
61	CST	10.0	*Furipterus horrens*

Roost	Type	Height	Species
62	CST	4.0	*Micronycteris megalotis*
63	EST	7.0	*Saccopteryx leptura*
64	EST	3.0	*Saccopteryx bilineata*
65	CST	4.0	*Phyllostomus elongatus, Carollia perspicillata*
66	EST	—	*Saccopteryx leptura*
67	FOL (UF)	1.0	*Choeroniscus minor*
68	other	5.0	*Saccopteryx bilineata*
69	CFT	0.0	*Furipterus horrens*
70	UFT	0.0	*Cormura brevirostris*
71	FOL (LT)	1.0	*Mesophylla macconnelli*
72	UFT	0.0	*Cormura brevirostris*
73	ABH	0.0	*Peropteryx pallidoptera*
74	CST	1.5	*Carollia perspicillata*
75*	CST	18.0	*Carollia perspicillata, (Lampronycteris brachyotis), (Trachops cirrhosus)*
76	CST	—	*Molossus rufus*
77	ABH	0.0	*Peropteryx pallidoptera*
78	TAN	5.0	*Lophostoma silvicolum*
79	CST	9.0	*Phyllostomus hastatus*
80	CST	—	*Saccopteryx bilineata*
81	CFT	0.0	*Furipterus horrens*
82	CST	—	*Carollia perspicillata*
83	UEB	0.0	*Phyllostomus elongatus*
84	CST	—	*Phyllostomus elongatus*
85	CST	—	*Molossus rufus*
86	CST	—	*Micronycteris microtis*
87	CFT	0.0	*Hsunycteris thomasi*
88	UEB	0.0	*Anoura caudifer*
89	CFT	0.0	*Hsunycteris pattoni*
90	CST	—	*Saccopteryx bilineata*
91	CFT	0.0	*Glossophaga soricina*
92	CST	3.0	*Carollia perspicillata*
93	CST	—	*Furipterus horrens*
94	UFT	0.0	*Cormura brevirostris*
95	ABH	0.0	*Micronycteris matses*
96	ABH	0.0	*Micronycteris microtis*
97	other	8.0	*Saccopteryx leptura*
98	EST	—	*Saccopteryx bilineata*
99	CST	—	*Carollia perspicillata*
100	FOL (LT)	—	*Rhinophylla pumilio*

Roost	Type	Height	Species
101	CFT	0.0	*Carollia perspicillata*
102	UEB	0.0	*Peropteryx pallidoptera*
103	EST	1.5	*Rhynchonycteris naso*
104	EST	1.0	*Rhynchonycteris naso*
105	CST	2.0	*Micronycteris hirsuta*
106	FOL (LT)	3.0	*Artibeus anderseni*
107	FOL (LT)	—	*Artibeus anderseni*
108	CFT	0.0	*Micronycteris microtis*
109	CFT	0.0	*Micronycteris microtis*
110	CFT	0.0	*Hsunycteris pattoni*
111	CST	4.0	*Saccopteryx bilineata*
112	CST	4.0	*Micronycteris hirsuta*
113	CST	—	*Phyllostomus elongatus, P. hastatus*
114	FOL (UF)	4.5	*Thyroptera tricolor*
115	FOL (UF)	4.0	*Thyroptera tricolor*
116	FOL (UF)	4.0	*Thyroptera tricolor*
117	FOL (UF)	3.5	*Thyroptera tricolor*
118	FOL (LT)	—	*Rhinophylla pumilio*
119	FOL (LT)	—	*Artibeus anderseni*
120	FOL (UF)	—	*Thyroptera tricolor*
121	FOL (UF)	—	*Thyroptera tricolor*
122	CST	20.0	*Glyphonycteris sylvestris*
123	FOL (LT)	—	*Mesophylla macconnelli*
124	ABH	0.0	*Micronycteris hirsuta, M. microtis*
125	EST	—	*Rhynchonycteris naso*
126	UEB	0.0	*Hsunycteris* sp. nov.
127	CST	—	*Saccopteryx bilineata*
128	EST	—	*Saccopteryx leptura*
129	CST	25.0	*Phyllostomus hastatus, Carollia perspicillata, Molossus rufus*
130	CFT	0.0	*Micronycteris microtis, Carollia brevicauda*
131	EST	8.0	*Saccopteryx leptura*
132	UFT	0.0	*Cormura brevirostris*
133	UFT	0.0	*Cormura brevirostris*
134	CST	4.0	*Micronycteris homezorum*
135	ABH	0.0	*Micronycteris microtis*
136	CFT	0.0	*Peropteryx kappleri*
137	UFT	0.0	*Peropteryx kappleri*
138	CST	—	*Saccopteryx bilineata*
139	FOL (LT)	—	*Mesophylla macconnelli*

Roost	Type	Height	Species
140	CST	—	*Glyphonycteris daviesi*
141	UEB	0.0	*Platyrrhinus infuscus*
142	CFT	0.0	*Furipterus horrens*
143	UFT	0.0	*Peropteryx leucoptera*
144	UFT	0.0	*Peropteryx kappleri*
145	ABH	0.0	*Micronycteris microtis, Carollia brevicauda*
146	FOL (LT)	—	*Artibeus anderseni*
147	UFT	0.0	*Peropteryx pallidoptera*
148	FOL (LT)	—	*Artibeus anderseni*
149	FOL (LT)	3.5	*Artibeus anderseni*
150	CST	3.0	*Lampronycteris brachyotis, Carollia perspicillata*
151	CST	4.0	*Saccopteryx leptura*
152	CFT	0.0	*Trachops cirrhosus*
153	CFT	0.0	*Trachops cirrhosus*
154	UFT	0.0	*Peropteryx pallidoptera*
155	UFT	0.0	*Cormura brevirostris*
156	CFT	0.0	*Peropteryx leucoptera*
157	CST	—	*Micronycteris microtis*
158	CFT	0.0	*Glossophaga soricina, Carollia brevicauda*
159	ABH	0.0	*Micronycteris microtis, Carollia brevicauda*
160	CST	—	*Phyllostomus elongatus*
161	ABH	0.0	*Micronycteris matses*
162	CFT	0.0	*Micronycteris microtis*
163	FOL (UF)	3.0	*Artibeus lituratus*
164	EST	2.0	*Artibeus obscurus*
165	CFT	0.0	*Micronycteris microtis, Carollia brevicauda*
166	UFT	0.0	*Peropteryx leucoptera*

APPENDIX 3

Roosting Habits of Amazonian Bats Based on Extralimital Observations[a]

Roost types are listed in alphabetical order with predominant roost type(s) in bold, if known. No predominant roost type is indicated if observations are too few or too ambiguous to distinguish relative frequencies of multiple known roost types, or when just a single roost observation is available.

	Roost type(s)	Reference(s)
EMBALLONURIDAE		
Cyttarops alecto	**FOL**	Starrett and Casebeer (1968)
Diclidurus albus	**FOL**	Goodwin and Greenhall (1961), Fenton et al. (2001)
Peropteryx kappleri	CFT, R/C, UFT	LaVal (1977), Handley (1979), Bradbury and Vehrencamp (1976)
Peropteryx macrotis	CST, R/C	Goodwin and Greenhall (1961), Handley (1979), Ibáñez (1981)
Rhynchonycteris naso	**EST**, FOL	Goodwin and Greenhall (1961), Bradbury and Emmons (1974), Ibáñez (1981)
Saccopteryx bilineata	**CST**, **EST**, R/C	Goodwin and Greenhall (1961), Bradbury and Emmons (1974), Ibáñez (1981)
Saccopteryx canescens	**EST**, TAN	Ibáñez (1981)
Saccopteryx leptura	**EST**, FOL, TAN	Goodwin and Greenhall (1961), Bradbury and Emmons (1974), Ibáñez (1981)
PHYLLOSTOMIDAE		
Anoura caudifer	**R/C**	Handley (1979), Campanhã and Fowler (1993)
Anoura geoffroyi	**R/C**	Goodwin and Greenhall (1961), Handley (1979)
Artibeus (D.) cinereus	**FOL**	Goodwin and Greenhall (1961), Machado et al. (2008)
Artibeus (A.) lituratus	CST, **FOL**, TAN	Goodwin and Greenhall (1961), Morrison (1980), Muñoz-Romo and Herrera (2003), Hernández-Mijangos (2010)
Carollia brevicauda	**CST**, FOL, **R/C**	Handley (1979)
Carollia castanea	**UEB**	Thies et al. (2006)
Carollia perspicillata	**CST**, FOL, **R/C**	Goodwin and Greenhall (1961), Handley (1979), Fleming (1988), Campanhã and Fowler (1993), Aguirre et al. (2003)
Chiroderma trinitatum	R/C	Goodwin and Greenhall (1961)
Chiroderma villosum	CST	Handley (1979)
Chrotopterus auritus	**CST**, **R/C**	Starrett and Casebeer (1968), Handley (1979), Medellín (1988)
Desmodus rotundus	**CST**, **R/C**	Goodwin and Greenhall (1961), Wilkinson (1985), Campanhã and Fowler (1993), Wohlgenant (1994), Aguirre et al. (2003)
Diaemus youngi	CST, R/C	Goodwin and Greenhall (1961)
Diphylla ecaudata	**R/C**	Handley (1979)
Gardnerycteris crenulatum	**CST**	Goodwin and Greenhall (1961), Handley (1979)
Glossophaga soricina	CFT, **CST**, **R/C**	Goodwin and Greenhall (1961), Handley (1979), Campanhã and Fowler (1993), Aguirre et al. (2003)

	Roost type(s)	Reference(s)
Glyphonycteris sylvestris	**CST**	Goodwin and Greenhall (1961), Handley (1979)
Lampronycteris brachyotis	**CST**	Goodwin and Greenhall (1961), Handley (1979), Weinbeer and Kalko (2004)
Lionycteris spurrelli	**R/C**	Handley (1979)
Lonchophylla mordax	CFT, CST	Armstrong (1969)
Lonchorhina aurita	**R/C**	Goodwin and Greenhall (1961), Handley (1979)
Lophostoma brasiliense	**TAN**	Goodwin and Greenhall (1961), York et al. (2008)
Lophostoma silvicolum	**TAN**	Handley (1979), Kalko et al. (1999)
Micronycteris hirsuta	**CST**	Goodwin and Greenhall (1961)
Micronycteris megalotis	CFT, CST, R/C	Goodwin and Greenhall (1961), Handley (1979), Ibáñez (1981)
Micronycteris microtis	CFT, CST, R/C	Handley (1979)
Micronycteris minuta	**CST**	Goodwin and Greenhall (1961), Handley (1979)
Micronycteris schmidtorum	**CST**	Handley (1979)
Mimon bennettii	CST	Allen (1911)
Phyllostomus discolor	**CST**, R/C	Goodwin and Greenhall (1961), Handley (1979), Wohlgenant (1994)
Phyllostomus elongatus	**CST**	Handley (1979), Ibáñez (1981), Aguirre et al. (2003)
Phyllostomus hastatus	**CST**, FOL, R/C	Goodwin and Greenhall (1961), Handley (1979)
Platyrrhinus fusciventris	CST, FOL	Goodwin and Greenhall (1961)
Rhinophylla pumilio	**FOL**	Zortéa (1995)
Tonatia saurophila	**CST**	Goodwin and Greenhall (1961)
Trachops cirrhosus	CFT, **CST**	Goodwin and Greenhall (1961), Armstrong (1969), LaVal (1977), Handley (1979), Kalko et al. (2006)
Trinycteris nicefori	**CST**	Goodwin and Greenhall (1961), Handley (1979), Weinbeer and Kalko (2004)
Uroderma bilobatum	**FOL**	Goodwin and Greenhall (1961), Timm (1987), Kunz and McCracken (1996)
Vampyrodes caraccioli	**FOL**	Goodwin and Greenhall (1961)
Vampyrum spectrum	**CST**	Ditmars (1935), Goodwin and Greenhall (1961), Vehrencamp et al. (1977)
MORMOOPIDAE		
Pteronotus gymnonotus	**R/C**	Sources cited by Patton and Gardner (2008)
Pteronotus parnellii	CST, **R/C**	Handley (1979)
Pteronotus personatus	**R/C**	Sources cited by Patton and Gardner (2008)
NOCTILIONIDAE		
Noctilio albiventris	**CST**, R/C	Handley (1979), Ibáñez (1981), Fenton et al. (1993), Aguirre et al. (2003)
Noctilio leporinus	**CST**, R/C	Goodwin and Greenhall (1961)
FURIPTERIDAE		
Furipterus horrens	CFT	LaVal (1977)

	Roost type(s)	Reference(s)
THYROPTERIDAE		
Thyroptera discifera	**FOL**	Robinson and Lyon (1901)
Thyroptera tricolor	**FOL**	Goodwin and Greenhall (1961), Findley and Wilson (1974), Vonhof and Fenton (2004)
NATALIDAE		
Natalus tumidirostris	**R/C**	Goodwin and Greenhall (1961), Handley (1979)
MOLOSSIDAE		
Cynomops abrasus	CST	Idoeta et al. (2012)
Cynomops planirostris	**CST**	Handley (1979), Idoeta et al. (2012)
Eumops hansae	CST	Handley (1979)
Eumops glaucinus	**CST**	Handley (1979), Aguirre et al. (2003)
Molossops temminckii	CST	Idoeta et al. (2012)
Molossus coibensis	**CST**	Handley (1979)
Molossus molossus	**CST**, FOL	Goodwin and Greenhall (1961), Ibáñez (1981), Aguirre et al. (2003)
Molossus pretiosus	**CST**	Ibáñez (1981)
Molossus rufus	**CST**, FOL	Goodwin and Greenhall (1961), Handley (1979)
Neoplatymops mattogrossensis	**R/C**	Handley (1979)
Nyctinomops laticaudatus	**R/C**	Goodwin and Greenhall (1961), Handley (1979)
Promops centralis	**FOL**	Goodwin and Greenhall (1961)
VESPERTILIONIDAE		
Eptesicus brasiliensis	**CST**	Handley (1979)
Eptesicus furinalis	CFT, CST	Handley (1979), Aguirre et al. (2003)
Lasiurus blossevillii	**FOL**	Goodwin and Greenhall (1961)
Myotis albescens	CST, **R/C**	Handley (1979)
Myotis nigricans	**CST**, **R/C**	Goodwin and Greenhall (1961), Handley (1979), Campanhã and Fowler (1993), Aguirre et al. (2003)
Myotis simus	**CST**	Myers and Wetzel (1979), Aguirre et al. (2003)
Rhogeessa io	**CST**, FOL	Goodwin and Greenhall (1961)

[a] Primarily from Central America, northern Venezuela, Trinidad, and southeastern Brazil.

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