BIOTROPICA 40(2): 203–210 2008 10.1111/j.1744-7429.2007.00362.x

Collpas: Activity Hotspots for Frugivorous Bats (Phyllostomidae) in the Peruvian Amazon

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ABSTRACT

In the SE Peruvian Amazon, large numbers of frugivorous bats regularly visit natural forest clearings known locally as *collpas* (which are also referred to as clay licks or mineral licks). Bats arrive at *collpas* to drink water that has accumulated in depressions created by larger geophagous mammals that consume exposed soil. Although *collpa* visitation is common, little is known about its causes and its ecological implications for the bat community. We compared patterns of use of *collpas* and non-*collpa* forest sites by bats in SE Peru. We mist netted bats at *collpas* and non-*collpa* sites during the dry season and compared abundance, species richness, species composition, sex ratio, and reproductive condition. More species were captured at *collpas* than at non-*collpa* sites, and *collpas* were visited almost exclusively by frugivores. Overall, bat-capture frequency and combined frugivorous bat-capture frequency were higher at *collpas* than at non-*collpa* sites, although some species of frugivorous bats were captured more frequently at non-*collpa* sites than at *collpas* (*e.g.*, *Carollia* spp.). Irrespective of capture site, more female bats were pregnant or lactating than not, but there was a distinct female sex bias in bats that visited *collpas*: 70 percent of bats captured at *collpas* were female, whereas 44 percent of bats captured away from *collpas* were female. These patterns suggest that *collpas* may provide important resources for frugivorous bats in SE Peru, just as they are thought to provide important resources to the vertebrates that consume *collpa* soils. Accordingly, *collpas* are important conservation targets in the region.

Abstract in Spanish is available at http://www.blackwell-synergy.com/loi/btp.

Key words: clay lick; conservation; mineral lick.

IN THE NEOTROPICS, SEVERAL SPECIES OF VERTEBRATES VISIT *COLLPAS* to consume soil (Emmons & Stark 1979). *Collpas* (MacQuarrie 2001, alternatively *ccolpas* [Burger & Gochfeld 2003])—also referred to as clay licks (Gilardi *et al.* 1999), mineral licks (Emmons & Stark 1979), natural licks (Klaus & Schmid 1998), and *saladeros* (Reid *et al.* 2002)—are open areas in the forest or on riverbanks where the soil is exposed. In the Peruvian Amazon, some birds (*e.g.*, cracids, parrots), monkeys (*e.g.*, black spider monkeys, red howler monkeys), ungulates (*e.g.*, collared peccaries, white-lipped peccaries, deer, tapirs), and small- to medium-sized rodents (*e.g.*, spiny rats, agoutis, pacas) have been observed consuming *collpa* soils (Emmons & Stark 1979, Terborgh 1983, Gilardi *et al.* 1999, Burger & Gochfeld 2003; A. Bravo & L. H. Emmons, pers. obs.). Potential explanations for geophagy almost unanimously hypothesize that animals seek a key resource that is available in greater concentration in *collpa* soils than elsewhere (Kreulen 1985). Postulated resources include mineral elements (Emmons & Stark 1979, Brightsmith & Muñoz-Najar 2004) and dietary supplements that bind plant secondary metabolites (Gilardi *et al.* 1999).

In addition to birds and nonvolant mammals, bats visit *collpas* in great numbers to drink water that has accumulated in depressions made by larger geophagous animals (A. Bravo & L. H. Emmons, pers. obs.; Fig. S1). Despite the prominence of this behavior, we know of only one published report (Tuttle 1974) and a published abstract (Reid *et al.* 2002) of similar phenomena. In an intriguing paper, Tuttle (1974) reported several species of stenodermatine bats visiting two 'water holes' in the Venezuelan Amazon that bear striking similarities to the *collpas* we have observed in Peru. These water holes were visited by tapirs with greater frequency than comparable natural pools. Tuttle (1974) reported that indigenous people who hunt tapirs in the region told him that the "noise made by the large numbers of drinking bats greatly hinders their hunting" at water holes frequented by tapirs. He also described stenodermatine bats visiting a single small pool on a rock that had been used a few days earlier for processing animal hides with borax and salts, to the exclusion of five similar pools on the same rock. *Collpa* visitation by bats was also explored in Ecuador, where the exposed soils are referred to as *saladeros* (Reid *et al.* 2002).

In this study, we compared patterns of use of *collpas* and non-*collpa* forest sites by bats in the Los Amigos river watershed in SE Peru. Specifically, we compared abundance, species richness, species composition, sex ratio, and reproductive condition of bats visiting *collpas* relative to comparable, non-*collpa* forest sites. Given the importance of frugivorous bats to seed dispersal and forest regeneration (*e.g.*, Fleming 1988), if *collpas* provide key resources for frugivorous bats, then these sites should be regarded as conservation priorities.

METHODS

STUDY SITE.—To compare patterns of use at *collpas* and non-*collpa* sites, we mist-netted bats from September through November 2005 in Los Amigos Conservation Concession, located at the confluence of Los Amigos and Madre de Dios rivers in the Department of Madre de Dios, SE Peru. This private concession protects about

Received 17 January 2007; revision accepted 16 June 2007.
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136,000 ha of Amazonian forest within the Moist Humid Ecological Zone (Holdridge *et al.* 1971); for a more detailed overview of the region see Terborgh (1983). The average annual temperature for 2000–2006 was 21–26°C, and average rainfall was 2700–3000 mm, unevenly distributed between the wet (October–April) and the dry (May–September) seasons (Centro de Investigación y Capacitación Rio Amigos, pers. comm.).

The SE Peruvian Amazon is a region with high bat diversity. Studies conducted in the Manu National Park, located adjacent to the west side of the Los Amigos Conservation Concession, have reported species-rich bat communities for the lowlands (Ascorra *et al.* 1991, Pacheco *et al.* 1993, Patterson *et al.* 1996, Voss & Emmons 1996). Community assemblages were composed mainly of species in the family Phyllostomidae, more specifically of the subfamily Stenodermatinae. For instance, Ascorra *et al.* (1991) reported 17 stenodermatine bats from a total of 44 species. Voss and Emmons (1996) reported 21 stenodermatine bats from a total of 60 species sampled. Based on this information, we expected a similar number of species as reported by the latter to be present in the study area.

We selected three major *collpas* located along the Los Amigos River (*Collpa* 1: 12°32′35″ S, 70°04′58″ W; *Collpa* 2: 12°30′23″ S, 70°08′55″ W; *Collpa* 3: 12°27′30″ S, 70°15′10″ W). *Collpa* size in the study area varied considerably, from < 1 m to *ca* 20 m along the longest axis. To minimize the effect of *collpa* size on bat activity among sampling sites, we chose *collpas* of similar size (*Collpa* 1: 17.4 × 8.3 m; *Collpa* 2: 18 × 7.6 m; *Collpa* 3: 16.3 × 10.2 m) located in mature flood plain forest at *ca* 1 km from the Los Amigos riverbank. To maximize our sampling area and to provide relatively independent estimates of bat activity patterns, *collpas* were spatially separated by > 8 km. At each *collpa*, the ground was mostly bare from the water edge to about 5 m, with only a few established shrubs and trees > 50 cm high. These individuals were presumably less vulnerable than smaller plants to trampling and browsing by large mammals. The absence of most vegetation is due to the activities of tapirs and large herds of peccaries that trample and/or root in the soil surrounding the *collpas*. Large mammals, such as peccaries and tapirs, were actively visiting the studied *collpas* (fresh tracks and observations). To compare bat activity at *collpas* with background activity in the forest, we established a non-*collpa* forest site in the same mature flood plain forest where its paired *collpa* was located. Each non-*collpa* forest site had comparable vegetation structure to its paired *collpa*, 400–500 m away, but lacked standing water.

Bat sampling.—We sampled bats weekly from September to November 2005. We captured bats using 6-m mist nets at three *collpas* and paired non-*collpa* sites. To ensure that our sampling was influenced by similar variation in weather and phases of the moon, we sampled both a *collpa*/non-*collpa* pair (in random order) before moving on to the next *collpa*/non-*collpa* pair.

We used distinct protocols for sampling bats at *collpas* and non-*collpa* forest sites. At *collpas,* we set a single net *ca* 1 m from the main water pool. This net captured all the bats that two people could process effectively. In contrast, we used six to ten mist nets deployed in a zigzag arrangement back-and-forth along and across a previously established human-made trail at each non-*collpa* forest site. We selected relatively open sites along the trails that bats may use as flyways, and avoided cluttered areas that bats likely avoid. The use of man-made trails is a standard technique to increase capture of bats in the forest interior (Jones *et al.* 1996), and allowed us to use forest sites with similar vegetation structure to the *collpas* we used in this study. We generally opened the nets for 6 h at night beginning at sunset (1730 h–1745 h) until midnight. Sometimes, however, we had to close the *collpa* net before midnight because of the extreme numbers of bats captured. To minimize moonlight effects on bat activity (Morrison 1978, Lang *et al.* 2006), we did not set nets five nights before or after a full moon. At *collpas* and at non-*collpa* forest sites, we checked nets every 15 min, and captured bats were placed into individual cloth bags. We identified each captured bat to the level of species using diagnostic characters provided by Emmons and Feer (1997), Reid (1997), Eisenberg and Redford (1999), LaVal and Rodriguez-H (2003), Velazco (2005), as well as museum specimens examined at the Museum of Natural Science of Louisiana State University prior to embarking on the field study. We recorded sex, reproductive status (*e.g.*, pregnant, lactating), age class (*e.g.*, juvenile, adult), weight, and forearm length of each bat captured; bats were rarely kept in cloth bags for > 30 min before processing, and never > 20 min for pregnant or lactating females. Each bat was banded with a stainless steel ball-chain necklace carrying a numbered aluminum band (Handley *et al.* 1991) before release.

Data analyses.—We compared bat activity—defined as the number of bats captured per net hour—at *collpas* and non-*collpa* forest sites. We calculated the mean and SE of bat activity and used a paired *t*-test in SAS to compare activity at *collpa* versus non-*collpa* sites (Zar 1999). We tested whether the proportional representation of frugivorous bats was independent of capture site with a chi-square test of independence (Sokal & Rohlf 1995). We compared bat species richness at *collpas* and non-*collpa* forest sites using rarefaction (Hurlbert 1971). We calculated the expected number of species for a given number of individuals in the program PAST (PAlaeontological STatistics, ver. 1.25, Ø. Hammer, D. A. T. Harper and P. D. Ryan, May 18, 2004) and constructed a rarefaction curve. We determined the similarity among all *collpas* and all non-*collpa* forest sites using the Bray-Curtis Index (also called the Sorensen Quantitative Index; Magurran 2004). In addition, using the same index, we determined the overall similarity between *collpas* and non-*collpa* sites. We compared species-rank abundance distributions of bats captured at *collpas* and non-*collpa* forest sites with a two-sample Kolmogorov–Smirnov test using SPSS (SPSS Inc. 1990).

In addition, we used chi-square tests of independence (Sokal & Rohlf 1995) to determine whether the proportions of female versus male bats, reproductively active versus non reproductive female bats, and pregnant versus lactating reproductive female bats were independent of site of capture. We used a binomial distribution to calculate the standard deviations of the categories analyzed, and chi-square goodness-of-fit tests (Sokal & Rohlf 1995) to determine whether the proportion of female versus male bats at each site of capture differed from 50:50.

RESULTS

BAT ACTIVITY AT *COLLPAS*.—Thirty-three of a total of 60 bat species reported for this region (Voss & Emmons 1996) were captured during the sampling period (30 nights and 710 total net hours; Table S1). All bats captured at *collpas* and non-*collpa* forest sites belonged to the family Phyllostomidae, predominately frugivores from the subfamilies Stenodermatinae and Carolliinae. The predominance of frugivorous species at *collpas* was significantly higher than at non-*collpa* forest sites ($\chi^2 = 80.1$; $P < 0.001$). At *collpas,* 99.8 percent of the individuals were members of 24 frugivorous species and only two individuals, one of *Desmodus rotundus* and one of *Tonatia* sp., were not frugivorous (Table S1). In contrast, at non-*collpa* forest sites, 90 percent of the individuals were frugivorous (Table S1).

Bat activity at *collpas* (number of bats/net/h) was significantly greater than at non-*collpa* forest sites ($t = 16.85$; $P < 0.01$; Fig. 1). Slightly more than 10 bats/net/h were captured at *collpas*, whereas < 1 bat/net/h was captured at non-*collpa* forest sites. Despite higher sampling intensity at non-*collpa* forest sites relative to the *collpa* sites (616 vs. 94 total open net hours), over ten times as many bats were captured at *collpas* (961 vs. 86; Table S1). The number of recaptured bats was very low at *collpas* as well as at non-*collpa* forest sites; only four individuals were recaptured in the former and one in the latter. This result confirms quantitatively that large numbers of bats congregate each night at *collpas*, where many bats were observed drinking the water that had accumulated in the soil depressions. It appeared that most bats arrived to a *collpa* from above the immediately adjacent canopy (as opposed to through the forest). They maneuvered to fly close to the water pool and once they were flying above the water body, they descended and ascended back and forth to drink water.

SPECIES RICHNESS.—Observed species richness was higher at *collpas* compared to non-*collpa* forest sites. Twenty-six species were captured at *collpas*, whereas only 18 species were netted at non-*collpa* forest sites (Table S1). The rarefaction analysis indicates that this difference in richness could be explained by the higher number of individuals captured at *collpas*. The rarefaction curves show that, for any given number of individuals, non-*collpa* forest sites have higher expected numbers of species than *collpas* (Fig. 2). Moreover, the accumulation curve of *collpas* has an asymptotic shape, indicating that the observed number of species was close to the total number of species visiting *collpas*, whereas the curve for non-*collpa* sites is not asymptotic, showing that the total number of species expected in the area was not sampled.

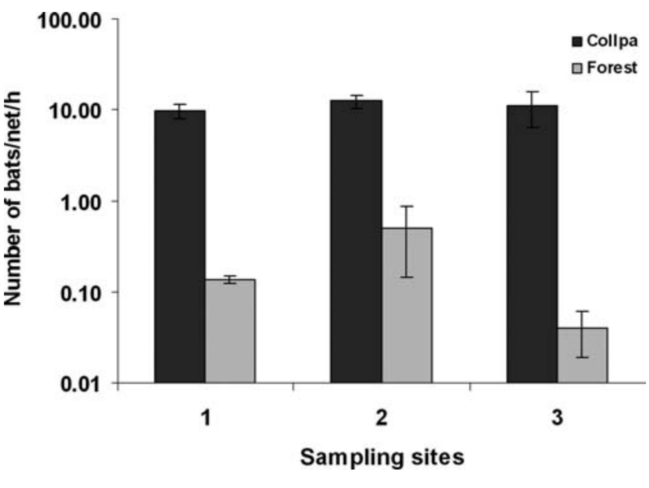

FIGURE 1. Bat captures (number of bats/net/h) ± SE for *collpas* and non-*collpa* forest sites in SE Peru.

SPECIES COMPOSITION AND ABUNDANCE.—The pattern of species similarities was consistent across *collpas* and non-*collpa* forest sites. The three *collpas* were more similar to each other than to any non-*collpa* site, and the same pattern was seen for the non-*collpa* forest sites (Table 1). In contrast, low similarities were found between *collpas* and non-*collpa* forest sites (Table 1). When the three samples for each category were pooled, the similarity index between *collpa* and non-*collpa* sites was 0.09. A total of 33 species were captured, with 11 species common to both sites, 15 species exclusively captured at *collpas*, and 7 species captured only in non-*collpa* forest sites.

The species-rank abundance distributions of bats differed between *collpas* and non-*collpa* forest sites (Kolmogorov–Smirnov $Z = 1.52$; $P = 0.02$; Fig. 3). At both types of sites, one very common species occurred. *Platyrrhinus helleri* represented 18 percent of the relative abundance at *collpas*, whereas *Carollia perspicillata* represented 17 percent of the relative abundance at non-*collpa* forest sites. In addition, three common species (> 10% relative abundance) were registered at *collpas* and non-*collpa* forest sites. *Uroderma bilobatum, Artibeus lituratus,* and *A. planirostris* were relatively common in the former, whereas *A. lituratus*, *Carollia brevicauda*, and *A. planirostris* were relatively common in the latter. Nevertheless, because of the higher species richness at *collpas,* more rare species occurred at these sites than at non-*collpa* forest sites. In fact, 12 of 26 species occurred at very low relative abundances at *collpas*: *Artibeus anderseni, A. cinereus, A. concolor, C. brevicauda, C. perspicillata, Mesophylla macconnelli, Platyrrhinus* sp., *Sphaeronycteris toxophyllum, Tonatia* sp., *Vampyressa pusilla, Vampyressa* sp., and *Vampyrodes caraccioli.*

BATS' SEX AND REPRODUCTIVE CONDITION.—At *collpas*, there was a strong female sex bias compared to non-*collpa* forest sites ($\chi^2 = 32.1$; $P < 0.0001$; Fig. 4A). More than 70 percent of bats captured at *collpas* were female ($\chi^2 = 209.4$; $P < 0.0001$), whereas about the same numbers of female and male bats were captured at non-*collpa* forest sites ($\chi^2 = 1.22$; $P = 0.26$).

More female bats were reproductively active (lactating and pregnant) than not at both *collpas* and non-*collpa* forest sites ($\chi^2 = 3.04$; $P = 0.08$; Fig. 4B). Nevertheless, no difference was found between the proportions of lactating and pregnant females for either type of site ($\chi^2 = 0.93$; $P = 0.34$; Fig. 4C).

DISCUSSION

BATS AND *COLLPAS*.—This study is the first to quantitatively confirm that *collpas* in the Peruvian Amazon are visited by frugivorous bats

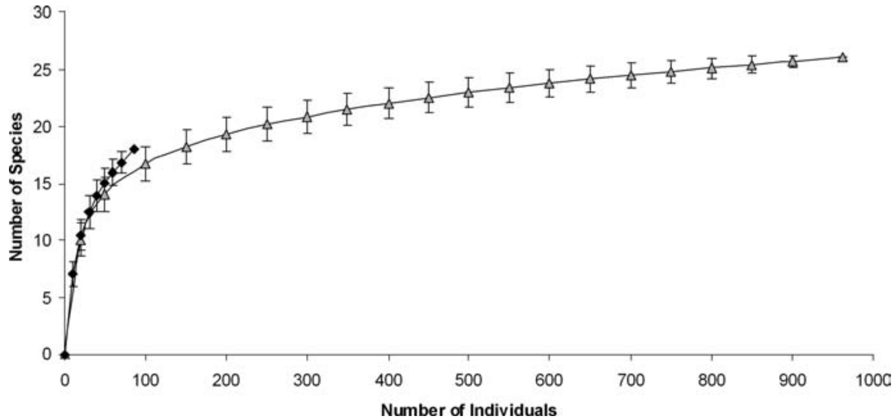

FIGURE 2. Rarefaction curves for bats visiting *collpas* and non-*collpa* forest sites in SE Peru. Curves represent the expected number of species for a given number of sampled individuals. Triangles represent the accumulation curve at *collpas*; diamonds represent the accumulation curve at non-*collpa* forest sites. Vertical lines represent ± SD.

in large numbers and out of proportion to their relative abundance in local bat assemblages. Although the sampling effort at non-*collpa* forest sites was almost six and a half times higher than at *collpas*, the total number of bats captured at *collpas* was more than ten times greater (Table S1; Fig. 1). This higher bat activity at *collpas* was due to large numbers of individuals of several frugivorous species. These results suggest that bat frugivory is associated with *collpa* visitation. In addition, our results show that stenodermatine fruit bats, which are noted dietary fig-specialists (Fleming 1986, Kalko *et al*. 1996), seem to be most strongly associated with this behavior.

Presumably, bat species at *collpas* and non-*collpa* forest sites belong to the same local community. Although more species were captured at *collpas*, rarefaction analysis indicates that this was only an effect of having captured more individuals there. Even so, species abundances differed dramatically between *collpas* and non-*collpa* forest sites. There was a clear bias of frugivorous species visiting *collpas* compared to non-*collpa* forest sites. At *collpas*, only two species, *D. rotundus* and *Tonatia* sp., with one individual each, were nonfrugivores. The sanguinivorous species, *D. rotundus*, may have been seeking large mammals that visit *collpas*, such as tapirs. In contrast, based on their major dietary components, six of 18 bat species were nonfrugivores at non-*collpa* forest sites. Thus, bat diversity at non-*collpa* forest sites comprises species from more feeding guilds than represented at *collpas*, *e.g.*, frugivores, gleaning carnivores, gleaning insectivores, nectarivores, and omnivores. Even though several omnivores, such as *Phyllostomus hastatus*, have a strong seasonal inclusion of fruits in their diets (Gardner 1977, Giannini & Kalko 2004), their ability to eat pollen, small vertebrates, and arthropods may reduce any advantage to them of visiting *collpas*. *Collpas* might also affect composition of captured bats by drawing species that normally fly high in the forest, down to where they get captured in ground level nets, as was suggested by Emmons *et al.* (2006) for pampa bat assemblages.

TABLE 1. *Bray–Curtis Similarity Index among three* collpas *and three non-*collpa *forest sites. Notice in bold the low similarities between each* collpa *and each non-*collpa *forest site.*

Sites	*Collpa* 1	*Collpa* 2	*Collpa* 3	Forest 1	Forest 2
Collpa 1					
Collpa 2	0.47				
Collpa 3	0.38	0.64			
Forest 1	**0.10**	**0.23**	**0.27**		
Forest 2	**0.04**	**0.08**	**0.11**	0.35	
Forest 3	**0.03**	**0.04**	**0.05**	0.33	0.38

At non-*collpa* forest sites, species of the subfamilies Stenodermatinae and Carolliinae were the most common components of the assemblage, a general pattern for bat communities in Neotropical forests (Ascorra *et al.* 1996, Patterson *et al.* 1996, Stevens *et al.* 2004). In contrast, the subfamily Carolliinae was not well represented at *collpas*, where the four most abundant species belonged to the subfamily Stenodermatinae (*P. helleri*, *U. bilobatum, A. lituratus*, and *A. planirostris*). Surprisingly, species of *Carollia*, which are usually common in SE Peru (Ascorra *et al.* 1996, Patterson *et al.* 1996), were not among the major component species at *collpas,* yet they were at non-*collpa* forest sites.

Collpas offer a unique opportunity for the study of rare species of bats. For example, although *Sphaeronycteris toxophyllum* has a low relative abundance at *collpas,* this species is even rarer in the forest and few records have been reported (Pacheco *et al.* 1993, Angulo & Diaz 2004). During the period of study, reproductive females of *S. toxophyllum* visited *collpas*. Six females were captured and five of these were pregnant. This result supports the hypothesis that *collpas* may offer important resources for reproductive female bats because even some otherwise rare species are concentrated at these particular sites.

WHY DO BATS VISIT *COLLPAS*?—*Collpas* in SE Peru clearly attract large numbers of frugivorous bat species (Phyllostomidae). Competition for limited resources generally keeps animals apart spatially or

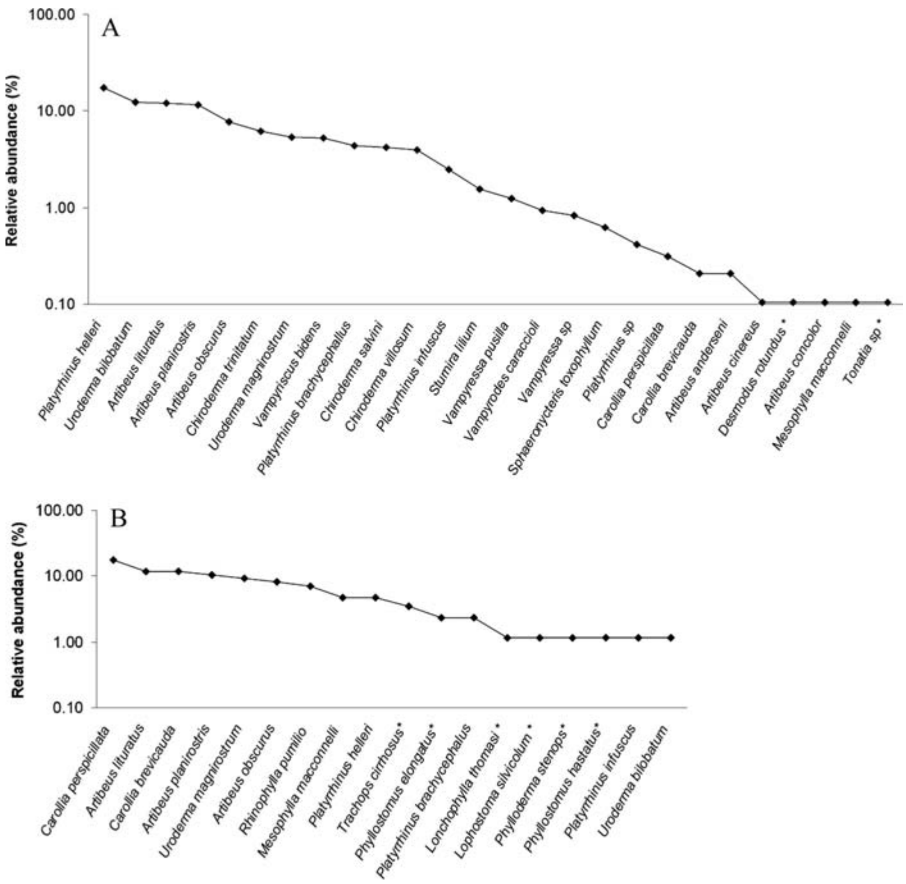

FIGURE 3. (A) Species composition and relative rank abundance of bats captured at *collpas*, and (B) bats captured at non-*collpa* forest sites. An asterisk indicates a nonfrugivorous species.

temporally, but certain limited resources can cause aggregations of animals. For instance, water draws bats to waterholes in arid landscapes (Stoner 2001, Adams & Thibault 2006), so water itself could potentially attract large numbers of bats to *collpas*, especially during the dry season. However, rivers, streams, and oxbow lakes are abundant in the lowland tropical forests of the Los Amigos watershed over the year, and frugivorous bats are not known to congregate at these bodies of water. Furthermore, frugivorous bats generally obtain nearly all their water from the fruits they eat (Fleming 1988, Studier & Wilson 1991, Wendeln *et al.* 2000). Thus, like other geophagous vertebrates, frugivorous bats may drink *collpa* water to obtain specific limiting nutrients, or clay to bind potential toxins.

Geophagy has been observed for many mammal and bird species worldwide (*e.g.*, Emmons & Stark 1979, Davies & Baillie 1988), but the reasons for this deliberate soil ingestion are still poorly understood. The hypotheses proposed to explain this behavior include ingestion of mineral supplements (Heymann & Hartmann 1991, Klaus & Schmid 1998), antidiarrheal agents (Mahaney *et al.* 1995), antacids (Davies & Ballie 1988), and substances that absorb dietary toxins (Kreulen 1985, Gilardi *et al.* 1999). The same hypotheses proposed to explain geophagy in mammals and birds could potentially explain why frugivorous bats drink water at the same licks. For instance, South American parrots may ingest soil to bind ingested plant's secondary compounds (Gilardi *et al.* 1999). Alternatively, parrots may ingest soil for nutrients (Brightsmith & Muñoz-Najar 2004), as do mammals from several vertebrate orders (*e.g.*, African savanna elephants, Asian proboscis monkeys, North American porcupines, South American white lipped peccaries, *etc.*) that preferentially ingest soil with high concentrations of sodium and/or calcium.

Collpa visitation by bats was strongly female biased in this study, a pattern also recorded in Ecuador by Reid *et al.* (2002). To fly and reproduce, bats have high nutritional requirements (Barclay 1994, Adams *et al.* 2003). Some species of bats seem to consume nutritionally complementary items, such as leaves, flower parts, nectar, pollen, and insects, to supplement their diets (Gardner 1977, Zortea & Lucena-Mendes 1993, Kunz & Diaz 1995). For instance, some bat species consume leaves that contain higher levels of calcium than some fruits of their diets (Ruby *et al.* 2000, Nelson *et al.* 2005). In addition, calcium, a mineral necessary to produce milk and a main component of bones, has been suggested as a limiting nutrient for female bats during reproduction (Barclay 1994, Studier & Kunz 1995, Adams *et al.* 2003); therefore bats may use secondary sources to obtain calcium. For example, in Colorado, large numbers

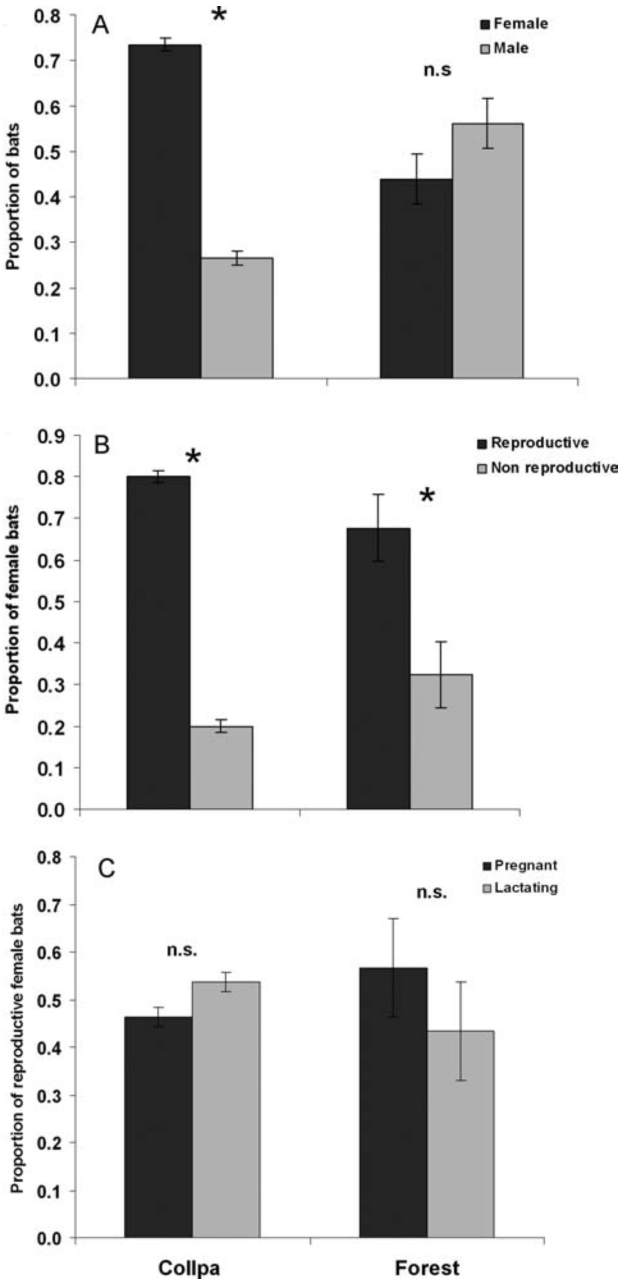

FIGURE 4. (A) Proportions of female and male bats at *collpas* and non-*collpa* forest sites; (B) Proportions of female bats in reproductive (pregnant and lactating) and non reproductive condition at *collpas* and non-*collpa* forest sites; (C) Proportions of female bats in reproductive condition that are pregnant or lactating at *collpas* and non-*collpa* forest sites. Error bars are SD from the binomial distribution. An asterisk indicates a significant difference ($P < 0.001$).

of female insectivorous bats in reproductive condition visit water pools in which the concentration of calcium is high compared to nonvisited pools (Adams *et al.* 2003). It is possible that the same phenomenon is being observed in SE Peru, where *collpas* may be providing mineral resources, such as calcium, for female frugivorous bats. However, whereas calcium is likely to be deficient in insectivorous diets (Bernard & Allen 1997), calcium is abundant in figs and other wild fruits (Oftedal *et al.* 1991, Wendeln *et al.* 2000), and it may be unlikely to be in short supply in frugivorous or herbivorous diets. If calcium were the nutrient sought by bats at *collpas*, then we would expect more *collpa* visitation by insectivorous, rather than by frugivorous bats (Adams *et al.* 2003). But calcium requirements for frugivorous bats increase significantly during reproduction and calcium provided by fig fruits may not be sufficient to cover these requirements (Barclay & Harder 2003). Thus, bats may use *collpas* as a secondary source of calcium. For instance, a fig-specialist *Pteropus conspicillatus* in New Guinea drinks sea water, which has been postulated to serve as dietary mineral supplementation for nutrients including calcium and sodium (Iudica & Bonaccorso 2003).

Another nutrient bats may be obtaining from *collpas* is sodium, which seems to be one of the most limiting nutrients to vertebrates in the midcontinental Neotropics (Stark 1970, Emmons & Stark 1979). As a consequence, low levels of sodium in some leaves (Ruby *et al.* 2000) and fruits consumed by bats could generate nutritional constraints for them. Wendeln *et al.* (2000) suggested that frugivorous bats in Panama may specifically select sodium-rich fig fruits to make up their sodium deficits. In addition, some studies worldwide suggest that the presence of high concentrations of sodium in the soil may drive its deliberate consumption by mammals and birds (Emmons & Stark 1979, Klaus and Schmid 1998, Brightsmith & Muñoz-Najar 2004). In SE Peru, Emmons and Stark (1979), Gilardi *et al.* (1999), and Brightsmith and Muñoz-Najar (2004) found high concentrations of sodium in the clay consumed by mammals and birds. These observations leave open the possibility of bats visiting *collpas* to drink water to obtain sodium to supplement their diets.

If *collpa* visitation by bats is related to mineral supplementation and female reproduction, two reasons may explain the low abundance of Carolliinae bats observed at *collpas*. First, it may be related to the *Piper*-specialist diet of species of *Carollia* (Fleming 1986, Kalko *et al.* 1996, Giannini & Kalko 2004). *Piper* fruits consumed by these bats have greater energetic and nitrogen content compared to some fig fruits, which are mainly consumed by stenodermatine bats (Herbst 1986, Fleming 1988). For instance, to satisfy the basic energy and nitrogen requirement of an individual of *C. perspicillata*, it has to consume about 33 and 12 fruits of *Piper amalago,* respectively. In contrast, if the diet switches to *Ficus ovalis*, the bat needs to consume 77 and 82 fruits for energy and nitrogen requirements, respectively (Fleming 1988). Even the basal metabolic rate (BMR) calculated for *Piper*-specialists is much higher than the BMR for fig-specialists (McNab 2003). However, information about nutrients besides nitrogen in *Piper* fruits, such as calcium and sodium, is not available in the literature. Thus, a *Piper*-specialized diet is not a conclusive explanation of the low number of species of *Carollia* visiting *collpas.* Second, low numbers of Carolliinae bats at *collpas* may be due to a temporal difference in reproductive season relative to other phyllostomid species captured at *collpas*. No female *Carollia* individuals were captured at *collpas*, and at non-*collpa* forest sites only two of seven female *Carollia* individuals were pregnant. Similarly, Wilson (1979) reported most of the Carollinae female bats captured in Peru in July–August as reproductively inactive. Just as we require more information on reproductive seasons and seasonal use of *collpas* by stenodermatine bats, more data are required to fully understand low rates of *collpa* visitation during the dry season by carolliine bats.

In conclusion, the large number of species and individuals of frugivorous bats visiting *collpas* suggests that *collpas* provide important resources to the community of frugivorous bats in the Peruvian Amazon, just as they do for several other vertebrate groups (Montenegro 2004). Additional research is necessary to determine potential reasons for this particular behavior, the role that *collpas* play in the ecology of bat communities in the area, and conservation decisions regarding these vertebrate communities and their resources. Furthermore, analyses of the mineral content of *collpa* water compared to other water sources in SE Peruvian Amazon likely will provide useful information to determine the reasons that bats visit and drink water from *collpas*. This study is a first step toward understanding the importance of *collpas* as key resources for frugivorous bats in SE Peru, with direct conservation implications for protecting a fully functional forest ecosystem.

ACKNOWLEDGMENTS

We extend our gratitude to the Peruvian Institute of Natural Resources (INRENA) for providing the research permit to do this study at Los Amigos Conservation Concession. We thank J. Rios, R. Gutierrez, N. Castro, and the rangers at ACCA for their help and enthusiasm doing fieldwork. We thank J. Eberhard, M. Hafner, J. Janovec, C. Meyer, N. Pitman, M. Tobler for their comments on the proposal that produced this study and for help with the logistics of the study. We especially thank S. Claramunt, J. Myers, G. Nunez, T. Paine, K. Stoner, and anonymous reviewers for their valuable comments on this manuscript. Financial support was provided by the Amazon Conservation Association, American Society of Mammalogists, Bat Conservation International, Biograds of Louisiana State University (LSU), Idea Wild, Louisiana Office of Environmental Education, LSU Graduate School, and the U.S. National Science Foundation.

SUPPLEMENTARY MATERIAL

The following supplementary material for this article is available online at: www.blackwell-synergy.com/loi/btp

Table S1. Species and captures of phyllostomid bats at *collpas* and *non-collpa* forest sites in SE Peru.

Figure S1. Phyllostomid bats visiting a *collpa* at the Amazon Conservation Concession (Photo: Courtesy of Mathias Tobler).

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