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-collpas sites during the dry season and compared abundance, species richness, sex ratio, and reproductive condition. More species were captured at collpas than at non-collpas 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-collpas sites, although some species of frugivorous bats were captured more frequently at non-collpa sites than at collpas. 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 where 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.

Key words: clay lick; conservation; mineral lick.

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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 (Ascórra 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, Ascórra 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 collpa sites 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 sizes 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 patterns, 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 (PAleontological 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-collpas. 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 reproductively 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 Carolliniae. 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 from above, 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.

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 collpas 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. Platyrhinus 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, Carolia brevipunctata, 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. brevipunctata, C. perspicillata, Mesophylla macconnelli, Platyrhinus sp., Sphaeronycteris toxophyllum, Tonatia sp., Vampyressa pusilla, Vampyressa sp., and Vampyrodus 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 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.
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 non-frugivores. 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, glean- ing insectivores, nectarivores, and omnivores. Even though several omnivores, such as Phyllostomus hastatus, have a strong seasonal in- clusion 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.

At non-collpa forest sites, species of the subfamilies Stenodermatinae and Caroliiinae 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 Caroliiinae was not well represented at collpas, where the four most abundant species belonged to the subfamily Stenodermatinae (P. belleri, 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.

**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.**

<table>
<thead>
<tr>
<th>Sites</th>
<th>Collpa 1</th>
<th>Collpa 2</th>
<th>Collpa 3</th>
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<th>Forest 2</th>
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<td>0.27</td>
<td></td>
<td></td>
</tr>
<tr>
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<td>0.08</td>
<td>0.11</td>
<td>0.35</td>
<td></td>
</tr>
<tr>
<td>Forest 2</td>
<td></td>
<td></td>
<td></td>
<td>0.33</td>
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<td>Forest 3</td>
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</table>

**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.
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 & Baille 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 & Baille 1988), and substances that absorb dietary toxins (Keulen 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, Zorrela & 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...
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 (Judica & 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), Gigardi 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 Carolliinae female bats captured in Peru in July–August as reproductively inactive. Just as we require more information on reproductive seasons and seasonal

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 ($P < 0.001$).
use of *collpas* by stenodermatine bats, more data are required to fully understand low rates of *collpa* visitation during the dry season by carolline 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.

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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).

LITERATURE CITED


