THE BAT FAUNA OF COSTA RICA'S RESERVA NATURAL ABSOLUTA CABO BLANCO AND ITS IMPLICATIONS FOR BAT CONSERVATION

LA FAUNA DE MURCIÉLAGOS EN LA RESERVA NATURAL ABSOLUTA CABO BLANCO (COSTA RICA) Y SUS IMPLICACIONES EN LA CONSERVACIÓN DE LA QUIROPTEROFAUNA

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ABSTRACT

Reserva Natural Absoluta Cabo Blanco, located at the southern tip of northwestern Costa Rica's Nicoya Peninsula, was established in 1963 and is the country's oldest nationally protected reserve. Because the climate of the Nicoya Peninsula is ideal for human habitation, the peninsula has been occupied for millennia and is a heavily impacted landscape. The region also is one of the most poorly studied in Central America in terms of biotic diversity. We initiated a multiyear survey of bats in the reserve and the adjacent Refugio de Vida Silvestre Cueva Los Murciélagos to quantify species diversity, abundances, habitat use, seasonality, and reproduction. By surveying bats during 5 rainy seasons and 4 dry seasons from July 1999 through February 2006, we address the following questions: Which species of bats are present in the area? Are the bat communities the same in 3 different habitats—coastal forest, inland forest, and limestone caves? Are the species diversity and abundances of bats in the rainy season similar to those in the dry season? Can we discern seasonal patterns of reproduction? Are the species diversity and abundances of bats at Cabo Blanco (a tropical moist forest in the Holdridge Life Zone classification) similar to those in the nearby tropical dry forest at Parque Nacional Palo Verde? What are the conservation implications of the bat assemblages found in this regenerating forest?

Using mist nets, searching for roosting bats, and an acoustical survey, 39 species of bats are documented in the area, including 5 emballonurids, 4 molossids, 1 mormoopid, 1 noctilionid, 21 phyllostomids, and 7 vespertilionids. The 2 most commonly captured bats, *Carollia perspicillata* and *Artibeus jamaicensis*, are abundant in both the inland and coastal forests and both are more abundant in the rainy season than in the dry season. Several species have clear habitat preferences, at least during the seasons in which we netted (*Glossophaga soricina* and *Uroderma bilobatum* along the coast and *Trachops cirrhosus* inland). The largest carnivores (*Noctilio leporinus*, *Chrotopterus auritus*, *Phyllostomus hastatus*, *Trachops cirrhosus*, and *Vampyrum spectrum*) are present, but the small and middle-sized predatory bats (*Micronycteris*, *Lophostoma*, and others)

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are poorly represented both in terms of diversity and abundance. We captured twice as many bats per hour of effort in the inland forest as we did in the coastal forest. The caves of Refugio de Vida Silvestre Cueva Los Murciélagos have 4 species of bats (*Balantiopteryx plicata, Saccopteryx bilineata*, *Desmodus rotundus*, and *Phyllostomus hastatus*) that are year-round residents.

Several species seem to be equally abundant in both seasons, including *Balantiopteryx plicata*, *Saccopteryx bilineata*, *Noctilio leporinus*, *Artibeus watsoni*, *Desmodus rotundus*, *Glossophaga soricina*, *Phyllostomus hastatus*, *Trachops cirrhosus*, *Lasiurus ega*, and *Myotis nigricans*. Our impression is that some species are more common during the rainy season than the dry season, but more data are needed to substantiate this assertion. Bats in the caves were equally abundant during each of our 8 cave surveys. *Desmodus rotundus* is the only species for which our data suggest year-round reproduction; we observed scrotal males, pregnant females, and juveniles during each of our visits to Cabo Blanco. Other species are present year-round but have seasonal reproductive activity. We captured *Artibeus watsoni* and *Carollia perspicillata* in both seasons but have seen pregnant females only during the rainy season.

Carollia perspicillata and *Artibeus jamaicensis* are the 2 most commonly captured bats at both Cabo Blanco and the nearby Parque Nacional Palo Verde. The species records and abundances of several other species differed between the sites, however. Species that are abundant at Palo Verde, but not yet recorded from Cabo Blanco, include *Pteronotus davyi*, *Pteronotus gymnonotus*, *Carollia subrufa*, *Centurio senex*, and *Natalus stramineus*. *Phyllostomus hastatus* is abundant at Cabo Blanco but not known from Palo Verde. Although both sites are relatively close together in the northern Pacific lowlands of Costa Rica, Cabo Blanco is substantially wetter, and the associated differences in vegetation may be driving bat distributional patterns.

We provide a number of new records and ecological information for bats on the Nicoya Peninsula and document that bat diversity and abundances can be substantial in regenerating forest. Several of the most commonly captured bat species are seed dispersers and may be critical to forest regeneration.

Key words: cave survey, Chiroptera, coexistence, community structure, feeding guilds, habitat fragmentation, Neotropics, regenerating forest, seasonality, species diversity.

RESUMEN

La Reserva Natural Absoluta Cabo Blanco, ubicada en el extremo sur de la península Nicoya de Costa Rica, se estableció en 1963 y es el área protegida más vieja del país. Dado a que el clima de la península Nicoya es ideal para la habitación humana y la producción de ganado, la península se ha habitado por miles de años y es una zona muy impactada en Centroamérica. Esta región también es una de las menos estudiadas en Centroamérica en cuanto a la diversidad biótica. Iniciamos un muestreo de murciélagos multianual dentro de la reserva y en el área adjunta, llamado el Refugio de Vida Silvestre Cueva Los Murciélagos, con el fin de determinar la diversidad de especies, abundancia, uso del hábitat, estacionalidad y reproducción. Después de haber hecho un muestreo a lo largo de 5 estaciones lluviosas y 4 estaciones secas desde julio 1999 hasta febrero 2006, investigamos las siguientes preguntas: ¿Cuáles especies de murciélagos están presentes dentro del área? ¿Existen diferencias en las comunidades de murciélagos

en 3 hábitats diferentes—bosque costero, bosque interno y cuevas calizas? ¿Existe una diferencia entre la estación seca y lluviosa en cuanto a la diversidad de especies y abundancia de murciélagos? ¿Hay patrones estacionales en cuanto a la reproducción? ¿Existe similitud en la diversidad y abundancia de murciélagos entre Cabo Blanco (un bosque húmedo tropical en la clasificación de Zonas de Vida Holdridge) y el vecino bosque seco tropical Parque Nacional Palo Verde? ¿Cuáles son las implicaciones a la conservación para los grupos de murciélagos que se encuentran en estos bosques en estado de regeneración?

Documentamos 39 especies de murciélagos en el área, incluyendo 5 especies de embalonúridos, 21 especies de filostómidos, 4 especies de molósidos, 1 mormoópido, 1 noctiliónido y 7 especies de vespertiliónidos. Las dos especies de murciélagos comúnmente capturadas, *Carollia perspicillata* y *Artibeus jamaicensis*, son abundantes tanto en bosques costeros como en bosques internos. Varias especies tienen preferencias a ciertos hábitats, por lo menos durante las estaciones de nuestras investigaciones (*Glossophaga soricina* y *Uroderma bilobatum* a lo largo de los bosques costeros y *Trachops cirrhosus* en los bosques internos). Los carnívoros más grandes (*Noctilio leporinus*, *Chrotopterus auritus*, *Phyllostomus hastatus*, *Trachops cirrhosus* y *Vampyrum spectrum*), están presentes, pero los murciélagos depredadores de tamaño pequeño y de tamaño mediano (*Micronycteris*, *Lophostoma* y otros) están pobremente representados. Capturamos dos veces más murciélagos por hora de esfuerzo en los bosques internos que en los bosques costeros. Las cuevas del Refugio de Vida Silvestre Cueva Los Murciélagos tienen 4 especies de murciélagos (*Balantiopteryx plicata*, *Saccopteryx bilineata*, *Desmodus rotundus* y *Phyllostomus hastatus*) que son residentes por todo el año.

Varias especies parecen ser igualmente abundantes en ambas temporadas, incluyendo *Balantiopteryx plicata*, *Saccopteryx bilineata*, *Noctilio leporinus*, *Artibeus watsoni*, *Desmodus rotundus*, *Glossophaga soricina*, *Phyllostomus hastatus*, *Trachops cirrhosus*, *Lasiurus ega* y *Myotis nigricans*. Nuestra impresión es que algunas especies son más comunes durante la época lluviosa que la época seca, pero se necesitan más datos para documentarlo. Los murciélagos en las cuevas fueron igualmente abundantes durante cada uno de los 8 muestreos de las cuevas. *Desmodus rotundus* es la única especie para que nuestros datos sugieron reproducción durante todo el año. Hemos observado machos reproductivos, hembras embarazadas y juveniles durante cada una de nuestras visitas a Cabo Blanco. Otras especies están presentes todo el año pero tienen una actividad reproductiva estacional. Capturamos *Artibeus watsoni* y *Carollia perspicillata* en ambas temporadas pero hemos registrado hembras embarazadas solamente durante la temporada lluviosa.

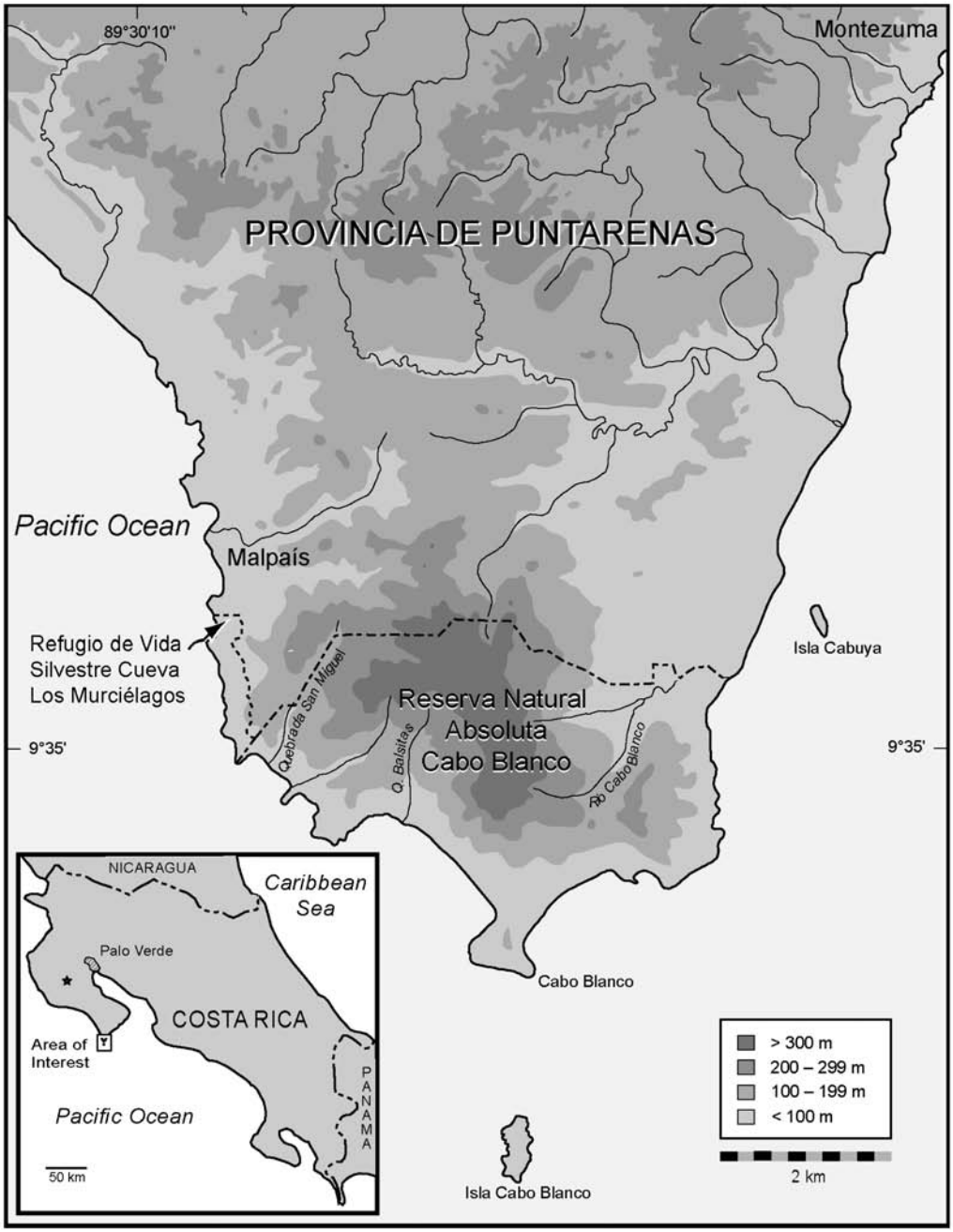
Carollia perspicillata y *Artibeus jamaicensis* son las 2 especies que se capturaron con más frecuencia en ambos Cabo Blanco y el vecino Parque Nacional Palo Verde. Sin embargo, los registros de especies y las abundancias de varias otras especies fueron diferentes entre los dos sitios. Las especies que son abundantes en Palo Verde pero aún no se registran en Cabo Blanco incluyen *Pteronotus davyi*, *Pteronotus gymnonotus*, *Carollia subrufa*, *Centurio senex* y *Natalus stramineus*. La especie *Phyllostomus hastatus* es abundante en Cabo Blanco pero no se registra en Palo Verde. A pesar de que los dos sitios están relativamente cerca uno del otro y en las tierras bajas del Pacífico norte de Costa Rica, Cabo Blanco es mucho más húmedo y las asociadas diferencias en la vegetación pueden ser responsables por dichos patrones de distribución de los murciélagos.

Proveemos nuevos registros e información ecológica para murciélagos en la península de Nicoya y documentamos que la diversidad y abundancia de los murciélagos pueden ser altas en bosques en proceso de regeneración. Varias de las especies de murciélagos capturadas más comúnmente son dispersores de semillas y por lo tanto pueden ser imprescindibles para la regeneración de los bosques.

Palabras clave: muestreo en cuevas, Chiroptera, coexistencia de especies, estructura comunitaria, gremios alimentarios, fragmentación de habitat, Neotropicó, bosque en recuperación, estacionalidad, diversidad de especies.

Costa Rica is one of the world's leading nations in establishing national parks and refuges, and currently more than 27% of the country's land surface is protected by government or private reserves. However, most of these reserves and wildlife refuges are relatively new, so the effects of former deforestation and land degradation are still evident even in well guarded areas. The oldest national reserve in Costa Rica is Reserva Natural Absoluta Cabo Blanco, at the extreme southern tip of the Nicoya Peninsula (Figs. 1, 2). This reserve was established in 1963, 7 years before the inception of Costa Rica's Servicio de Parques Nacionales, through the initiative and efforts of the Scandinavian emigrants Nicolas Wessberg and Karen Mogensen. They raised $30,000 in private funds to purchase the initial 1,172 ha. Later that year, the president of Costa Rica, Francisco Orlich Bolmarcich, declared the land a national reserve by executive decree. As an absolute reserve, no visitors were allowed, and no scientific investigations or photographs were permitted. The only official mandate was protection from the trio of threats—fire, timber harvesting, and poaching. Wessberg served as the reserve administrator without pay until he was murdered on the Osa Peninsula in 1975. In 1982, the reserve's original area was increased to include the first 1 km out from the shoreline, thus protecting 1,750 ha of ocean. Today, the reserve has expanded to cover 56,350 ha of marine area off Costa Rica's Pacific coast. The strict isolation of the reserve has eased in recent years, first with a government decree in 1988 opening the Cabuya (eastern) sector to the public and second with the opening of the San Miguel (western) sector to selected educational groups in 1999. Detailed overviews of the creation of

Figure 1 (facing page). Map of the southernmost tip of the Nicoya Peninsula showing the locations of Reserva Natural Absoluta Cabo Blanco and Refugio de Vida Silvestre Cueva Los Murciélagos in relation to the communities of Malpaís and Montezuma. Our netting along the coast was conducted between the Quebrada Balsitas and the unnamed stream immediately to the west. Our inland nets were set along the Quebrada San Miguel about a km from its mouth. The main building of the Estación Biológica San Miguel is located just east of the mouth of the Quebrada San Miguel. On the countrywide map, Parque Nacional Palo Verde (84 km to the north of Cabo Blanco) is indicated by cross hatchings and the community of Nicoya (near the base of the Peninsula) by the star. In 2005 the Ministerio del Ambiente y Energía (MINAE) acquired about a third of the private property that included Refugio de Vida Silvestre Cueva Los Murciélagos Reserva Natural Absoluta Cabo Blanco, including the bat caves and all land bordering the coast; the remainder of the property was acquired by a private landowner.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PROVINCIA DE PUNTARENAS
Pacific Ocean
Malpais
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Absoluta
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9°35'
9°35'
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NICARAGUA
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100 – 199 m
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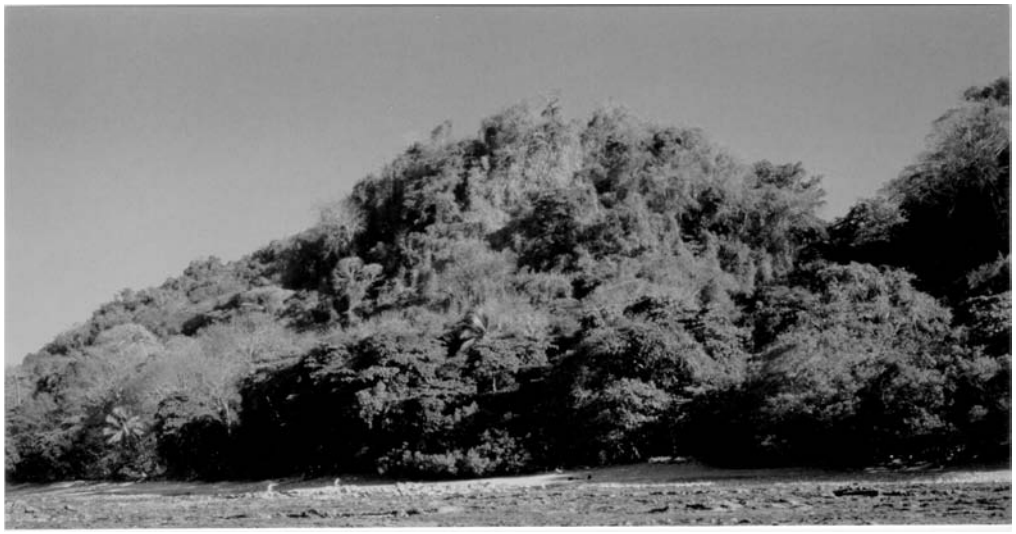

Figure 2. View of Reserva Absoluta Cabo Blanco taken from the Laguna San Miguel intertidal zone during the dry season of 2000. Note the rough terrain, the closed canopy of the 40-year-old secondary forest, and the scattering of leafless deciduous trees silhouetted against the sky.

Costa Rica's park service that emphasize the political and cultural history have been provided by Wallace (1992) and Evans (1999).

We have had the opportunity to survey bat distributions and abundances in the reserve in conjunction with our teaching efforts with the Organization for Tropical Studies over the past several years. Our goals herein are to document the recent history and the bat fauna of Reserva Natural Absoluta Cabo Blanco, focusing on the western sector around Estación Biológica San Miguel and the nearby Refugio de Vida Silvestre Cueva Los Murciélagos. We focused our survey on the following questions. What species are present in the area? Are bats equally abundant and diverse in 3 different habitats—the forest along the coast, inland forest, and limestone caves? Are the species diversity and abundances of bats in the rainy season similar to those in the dry season? Are there seasonal patterns in reproduction? Are the bat communities at Cabo Blanco and nearby but ecologically distinct Palo Verde similar?

Documentation of the bat fauna at the southern tip of the Nicoya Peninsula is valuable because this is one of the most poorly studied regions in Costa Rica, the region has been impacted by humans for several millennia, and our results have implications for bat conservation in Costa Rica as well as other areas in the Neotropics. Because the forest is regenerating and most species of mammals have received excellent protection for the past 4 decades, the forest and its wildlife species are in a state of rapid transition. Understanding how bats respond to conservation efforts will provide insights valuable to future conservation programs because bats play major roles as seed dispersers, pollinators, predators, and prey in the Neotropics.

METHODS

The information presented here comes from our survey studies and observations in and around Reserva Natural Absoluta Cabo Blanco, Puntarenas Province, Costa Rica. Our primary study sites are in the general vicinity of Estación Biológica San Miguel (9° 35' N, 85° 08' W) and the adjacent private reserve, Refugio de Vida Silvestre Cueva Los Murciélagos (9° 36' N, 85° 09' W) (Fig. 1). We have been working and teaching in the reserve regularly since 1999. For the bats, all linear measurements in the accounts that follow are in millimeters and weights are given in grams. Forearms (fa) were measured to the nearest 1 mm from the proximal extension of the radius–ulna (elbow) to the distal-most extension of the carpals (flexed wrist). Individuals categorized as adults are those with complete fusion of the epiphyses of metacarpals and phalanges. We recognize that some species of bats are more likely to be netted than others and that we are under-sampling the aerial insectivore community. Our characterizations of species as being abundant or uncommon refer to their presence as determined by our netting and survey techniques.

The focus of these accounts is the information we obtained between February 2000 and July 2003. The standard procedure in each netting session was to spend 1 night netting in the forest along the coast and 1 night in the forest inland (from sundown, ca. 1800 h, until after midnight). The coastal and inland sites are approximately 750 m apart, as the bat flies; the inland site is located on a ridge (ancient terrace) at ca. 70 m elevation. Occasionally, we would experience heavy rains after an hour or 2 of netting and would then resample that site for a second night. The number of nets used in specific locations was standardized across years, as was net placement. Depending on conditions (e.g., level of water in the stream over which we placed nets), we might add or delete one of the standard nets. We used more nets along the coast (30 or 42 m of net) than we did inland (18 or 24 m of net) because the inland ridge is considerably denser with vegetation than the coastal forest. Two of our standard net positions on the ridge were over a small stream, Quebrada San Miguel, and the third was across the trail approximately 20 m from the first stream crossing. We calculate our captures as bats per running meter of net per hour to standardize sampling, because we used a combination of 6- and 12-m mist nets at the sites. Data on capture rates and habitat preferences are from 4 rainy seasons (2000, 2001, 2002, and 2003) and 1 dry season (2001). Data from the rainy season 1999 and dry seasons of 2000, 2003, and 2006 are incorporated into the species accounts and inventory, but are not included in the analysis of habitat preferences because the sampling regime differed. In summary, we have netting data from 16 complete evenings, more than 12 partial evenings, 8 cave surveys, and numerous incidental observations over the 6-year period.

Bats were individually marked on a temporary basis with a black felt marker, and no recaptures in the same netting session are included. Data were analyzed using JMP and Minitab software. Habitat preferences are presented with and without Bonferroni corrections (Zar, 1996). For all of our analyses, we make the assumption that each capture is an independent event, in other words that bats are not captured in social groups and that we are not capturing the same individual from one year to the next. Additional netting was undertaken at selected sites, including several places over the Quebrada San Miguel, during both the rainy season and dry season.

Refugio de Vida Silvestre Cueva Los Murciélagos was a private reserve, adjacent to Reserva Natural Absoluta Cabo Blanco, and acted as a buffer area between the

reserve and the community of Malpaís (Fig. 1). The property along the coast was obtained by Ministerio del Ambiente y Energía (MINAE) in 2005; it is thus protected albeit not part of Reserva Natural Absoluta Cabo Blanco. There are 3 caves on this property and another cave just to the north along the beach on private property. All 4 caves are formed from heavily eroded limestone that has been uplifted at an oblique angle. For the purposes of our surveys, we worked primarily in the 3 southernmost caves which were originally part of Refugio de Vida Silvestre Cueva Los Murciélagos. We numbered these cave 1 (the northernmost cave), cave 2 (the center cave), and cave 3 (the southernmost cave). Cave 1 is a simple, closed-end, relatively dark passageway with a small entrance. The cave was formed by water eroding the tectonically uplifted limestone. Because this cave lies only a few kilometers east of the subduction zone of the Cocos Plate, the limestone has been upthrust vertically at nearly a 90° angle to the ground level. This cave runs parallel (north–south) to the subduction zone. Cave 2 is a closed-end passage, with a small entrance that opens up into a large cavern within a few meters of the entrance. It also was formed by water eroding the uplifted limestone. This cave is not as dark as cave 1 and runs east–west. Cave 3 is a large open natural limestone arch with dark, closed-end side passages; most of the bats roosted in the dark side passages. The cave was formed by a combination of water eroding the limestone and the sloughing of massive limestone blocks from the ceiling. The cave on private property, cave 4, faces west toward the ocean and is considerably brighter than the other caves. Several areas of the ceiling are open allowing light throughout the cave. Caves 2, 3, and 4 lie perpendicular to the subduction zone. Caves 1–3 were censused visually 8 times over the 6 years and we attempted to disturb the bats as little as possible. At least 1 individual of each species of bat roosting in the caves was captured to confirm identifications. In our 8 surveys, we observed only a single bat that was not identified to species; it was a small phyllostomid that was roosting by itself. Before we entered the caves, we located roosting bats and identified those near the entrance to species. Then, as we entered the cave, 2 people were responsible for counting or estimating the number of bats present in deeper sections. We recorded temperature (to the nearest 0.1°C) using a Raytek long-range digital thermometer both throughout the caves and in the vicinity of roosting individuals or groups of bats and noted the approximate locations of all individuals.

Complementing the mist net and roost site surveys, we also incorporate the results of an acoustical survey. In late February 2005, Richard K. LaVal conducted a 4-night acoustical survey near the Estación Biológica San Miguel using the Anabat bat-detecting system (Titley Electronics, Ballina, New South Wales, Australia) to detect and identify ultrasonic signals from free-flying bats. Two nights of this survey were conducted in the vicinity of the field station buildings in a more open area than either of our netting surveys, and two nights were conducted along the Quebrada San Miguel. Both sites were relatively close (ca. 0.75 km) to our netting area along the coast.

Only 2 other mammalogists, Richard LaVal and Bernal Rodríguez, have worked at Cabo Blanco previously; both were there for just a few days. They provided us with a number of observations that we incorporate into the following species accounts. Reference specimens of selected species are deposited in the mammal collection of the Museo Nacional de Costa Rica (MNCR), San José and the University of Kansas Natural History Museum (KU), Lawrence, Kansas. Additional specimens from the region are deposited in the collections of the Museo Nacional de Costa Rica (MNCR), San José and the University of Michigan Museum of Zoology (UMMZ), Ann Arbor.

Selected species (i.e., *Diclidurus albus*, *Vampyrum spectrum*), not otherwise vouchered, are documented with photographs. Carcasses of 2 species of bats (*Desmodus rotundus* and *Phyllostomus hastatus*) located in the caves were saved as vouchers.

Genera are listed alphabetically within families and species alphabetically within genera. Recent phylogenetic treatments of the family Phyllostomidae (Wetterer et al., 2000; Jones et al., 2002; Baker et al., 2003; and references therein) document that the traditional classification of subfamilies and genera within the leaf-nosed bats needs to be reassessed. Recent overviews, keys, biogeography, and literature reviews of Costa Rican bats may be found in Reid (1997), Timm and LaVal (1998), Rodríguez-H. and Wilson (1999), Timm et al. (1999), LaVal and Rodríguez-H. (2002), and Wilson et al. (2002).

RESULTS

Site History and Description

Overview of Nicoya Peninsula. The Nicoya Peninsula is part of the Central American Pacific lowlands, much of which is classified as dry forest in the Holdridge Life Zone system (Holdridge, 1967; Holdridge et al., 1971; Herrera and Goméz, 1993). The main body of the peninsula is composed of underlying basalt and limestone (Tournon and Alvarado, 1997; Denyer and Kussmaul, 2000) with moderate relief (highest hill 1,000 m, average hills 600 m) (Bergoeing, 1998). Reserva Natural Absoluta Cabo Blanco, on the tip of the peninsula, consists of Pliocene and Pleistocene sedimentary deposits (Vásquez, 1983; Tournon and Alvarado, 1997). The mean annual temperature in the reserve is 28°C. The mean annual precipitation is 3,100–3,200 mm (higher than rainfall at the base of the peninsula), with a strong dry season from January through March—this qualifies the tip of the peninsula as tropical moist forest (Herrera, 1985; Lindquist, 2003; Lindquist and Carroll, 2004).

In order to understand the current status of the peninsular biota, a consideration of land use history is warranted. Most ecologists and archaeologists have abandoned the notion that Neotropical landscapes at the time of European contact were pristine or virgin wilderness little affected by human agency (Denevan, 1992; Bush and Colinvaux, 1994; Clark, 1996; Stahl, 1996; Kennedy and Horn, 1997). A treatment of land use history should therefore incorporate what is known of human/ecosystem interactions of the last few millennia. In the case of the Nicoya Peninsula, the available evidence indicates a long and complex history.

Culturally and with reference to archaeological study, the Nicoya Peninsula has been considered a part of lower or southern Central America (Linares, 1979; Fonseca Zamora, 1993), the southern end of Mesoamerica (Creamer, 1987; Sluyter, 1994), the southern frontier of Mesoamerica (Quesada López-Calleja, 1980), part of the Isthmo–Colombian Area (Snarskis, 2003), and/or a part of an Intermediate Area or buffer zone between Olmec and Mayan influences to the northwest and Incan influences to the southeast (Stone, 1977; Lange, 1984). Within Costa Rica, the peninsula is considered to be a component of the Greater Nicoya archaeological subarea (Lange, 1984), which is one of 3 major zones within Costa Rica (the others are the Diquís southern Pacific subarea and the Central Highlands/Atlantic Watershed subarea) (Stone, 1977; Snarskis, 1981; Quilter, 2004). Scattered evidence indicates human presence along the Pacific

coast of Central America for the last 11,000 years (Cooke and Ranere, 1992).

Various authorities have written about the lives of the indigenous people of the Nicoya zone in the centuries before 1500. Collectively often referred to as the Chorotega, these people consisted of several different groups with distinct languages (including Pipil and Nicarao traders and settlers) (Fowler, 1985, 1991). Evidence exists for long and medium-distance trade, the former from Ecuador (Stone, 1977) and the latter along the Pacific coast in both directions and across the Golfo Nicoya between the mainland and the peninsula (Creamer, 1992). Based on interpretation of pottery remains, early (500 BC–600 AD) associations with people in the Central Highlands of Costa Rica seem to have waned by 1300 AD (Sheets et al., 1991). The best known archaeological site on the peninsula is Las Huacas, a large cemetery near the center of the peninsula (south of the town of Nicoya) that was excavated by the Swedish botanist Carl Hartman in the early 20th century (Hartman, 1907). He attempted to establish a stratigraphy of the remains in a desperate race against the looters that have plagued Costa Rican archaeological research for the last century (Lange, 1976; Skirboll, 1984). Las Huacas dates from the Early Polychrome Phase (= early Period V, 500–800 AD) and contains pottery, effigy grinding stones, and jade ornaments. The tradition of jade work on the Nicoya Peninsula evidently comes from Guatemala (Easby, 1968), but the source of the jade has not been definitively identified. A local (Nicoya) jade source has been postulated (Lange et al., 1981; Snarskis, 2003), but not located. A shift from jade to gold as a precious material occurred throughout Costa Rica around 500 AD, with metallurgy techniques introduced from Peru (Snarskis, 2003); the creative center of goldwork was in the Diquís rather than the Nicoya subarea (Bray, 1981). Clearly the people who lived in this region were influenced by both the well-studied Olmec/Maya and Inca civilizations by which they are bracketed geographically; nevertheless, one should not overlook the "uniquely innovative character" of the Greater Nicoya cultures (Abel–Vidor, 1981).

Several prominent archaeological investigations of the Nicoya area address population size, social organization, and diet of the indigenous people before and after contact with the Spanish invaders and settlers. First-hand descriptions by early European chroniclers also add to our knowledge. These sources, when pieced together, provide a revealing (albeit incomplete) narrative of the changes in natural resource use and availability over time. The Nicoya Peninsula (particularly at its base) is considered to have been moderately, but not highly populated for several thousand years prior to Spanish contact (Abel–Vidor, 1981). Trade and agricultural activities were concentrated along the shores of the Golfo Nicoya and the larger islands (especially Chira) within the gulf (Radell and Parsons, 1971). Social organization was in tribal groups rather than the chiefdom system associated with a distinct hierarchy of power, division of labor, and high population density (Creamer and Haas, 1985). Metates with evidence of corn-grinding wear (as opposed to ceremonial metates) have been found on the peninsula and date to the middle of Period IV (about 500 BC) (Snarskis, 1982), but other authorities push maize agriculture in the area as far back as 1800 BC (Hoopes, 1991). Maize and palm nut remains also are found in association with the jade-producing sites of 300 BC–500 AD (Snarskis, 2003), although the presence of wildlife bones at various peninsular locations throughout the centuries indicates a continued reliance on forest game (Kerbis, 1980). Household and hunting gardens (Linares, 1976) are known from other Central American areas and may have been in use here as well. Large scale clearing of forest probably did not occur, and building

materials for houses and rafts would have been smaller diameter trees rather than the forest giants (L. Gómez, pers. comm.; but see Piperno and Pearsall (1998) for evidence of large scale deforestation around 9,000 BC at the Yeguada site in Panama).

Extensive use of shellfish (for food and for dye) and of fish from the gulf is indicated by large shell middens dating from 500 AD and also from the Middle Polychrome Phase (= late Period V, 800–1200 AD) (Kerbis, 1980; Snarskis, 2003). Curiously, however, exploitation of marine resources seems to have been intermittent (Moreau, 1984) and may have been associated with regional climate change (Messenger, 1991). Use of shellfish was "not characteristic" of the people living on the tip of the peninsula (Moreau, 1984), possibly because this zone had neither the nutrient-rich upwelling currents found further north along the coast (Hubbs and Rodden, 1964) nor the coastal mangrove forests that serve as shellfish hatcheries along the gulf coast.

One of the earliest Spanish chronicles of the post-contact era is that of Gonzalo Fernández de Oviedo y Valdés (simply Oviedo in most accounts), who traveled throughout the Peninsula in 1527, while his ship was being repaired on Isla Chira. He reported scattered plantings of cacao (see also Bergmann, 1969), many birds and large mammals, and 2 different types of corn planted by the local people, one of which was a dry season corn that matured in 40 days and provided sustenance while the rain-dependent corn was still growing (Oviedo, 1959 IV:423). He also commented on the varied diet (including deer, roasted toads, and fruit of forest trees) of the local people, the pearls gathered from the gulf, and the lustrous pottery of Chira (Oviedo, 1959 III:298–299).

The arrival of the Spanish to a particular New World location was accompanied by, and often preceded by, the arrival of Old World diseases (Lovell, 1992). Indigenous populations in the Nicoya area were greatly reduced by disease and the slave trade. A reduction in population of 90% is indicated for Nicaragua (including the Nicoya area) between 1500 and 1600 (Newson, 1982). The Spanish used the islands in the Golfo Nicoya to load slave ships with destinations in Panama and Peru. This trade led to the establishment of several shipbuilding sites in the region, with attendant mainland tree-cutting to supply wood (Radell and Parsons, 1971).

In the mid-16th century Nicoya (and the rest of Costa Rica) were parts of the Kingdom of Guatemala. It was common practice for Spanish citizens to buy government posts in order to profit from independent activities such as forced labor, smuggling, and control of trade routes (Patch, 1994). During this time, Costa Rica was not considered to have any prospects for income enhancement and the records indicate that no one ever offered to buy the post. Because the Costa Rica post (covering what is present-day central and eastern Costa Rica) was close to the isthmian crossing, and therefore strategically important, the Spanish crown was impelled to pay a salary to the holder of this position. The Nicoya post was marginally more profitable because of pearl fishing in the gulf, but there were not enough indigenous people in the area to sustain an encomienda economy (Patch, 1994).

Costa Rican government historical documents provide data on crops, livestock, and human populations for individual administrative units in the country. Large-scale cattle and mule ranches were concentrated along the northeastern (upper gulf side) of the Nicoya Peninsula during the 1600s (Molina and Palmer, 2000). In 1765, the Correximiento de Nicoya contained 1 small pueblo of about 50 Indian families "y pocas menos de gente Ladina, pobres," with the rest of the region consisting of haciendas for raising cattle, mules, and horses. Salaries were paid in silver, clothing, and cacao

(Fernández, 1976:125). In 1884, the Nicoya canton (distal half of the peninsula, including the town of Nicoya) produced some corn and sugarcane, a substantial amount of rice, and no coffee, wheat, or potatoes (Meléndez Chaverri, 1978:47–57). In 1904, this canton had a population of "10,750 habitantes dedicados a la agricultura, a la ganadería y a la pesca" (Noriega, 1924:161), many of whom lived in and around the town of Nicoya.

First-hand descriptions of the distal half of the Nicoya Peninsula by naturalists and travelers of the late 19th and early 20th centuries emphasize the hilly and forested nature of the terrain. In 1881, J. F. Bransford searched for a local source of the jade used in the numerous carvings found on the peninsula. He camped along the Río Nosara, west of the Las Huacas site, and said of his surroundings, "We were in the finest forest I had ever seen. Apparently not one of the magnificent trees in this valley had been cut since the conquest, except where for an acre or so in 2 places clearings had been made. The undergrowth was scanty, while high overhead there was a dense canopy supported by superb columns" (Bransford, 1884:815). The Swedish naturalist Carl Bovallius visited Nicoya in 1882 and wrote "la Península de Nicoya, ancha y montañosa…sus colinas recubiertas de bosques" (Zeledón Cartin, 1997:90). In 1905, the German naturalist Karl Sapper stated that the western and southwestern sides of the peninsular tip were characterized by "las selvas vírgenes," abundant game, and hunting trails through the forest and down to the coast (Zeledón, 1998:57). As recently as 1915, large parties of wealthy hunters from San José crossed the gulf and rented horses for the occasion, hunting deer (*Odocoileus virginianus*), the large, highly prized rodent the tepezcuintle or paca (*Cuniculus* (*Agouti*) *paca*), and fowl (L. Gómez, pers. comm.). Photographs from the time show forested backdrops to these expeditions.

The picture that emerges of land use on the Nicoya Peninsula in general can be summarized as follows: 1) moderate but fluctuating settlement sizes for several thousand years (before 1500), with exploitation of coastal and forest resources, clearings for agriculture, but probably no large scale deforestation, 2) depopulation, land abandonment and/or a shift of population centers, and the introduction of Old World crops and livestock during the 2 centuries following contact with the Spanish (Whitmore and Turner, 1992), 3) subsistence agriculture, some larger plantations, and livestock raising on the peninsula (Gundmundson, 1983), but with most of the backbone of the peninsula remaining forested for the next 250 years (based on first-hand accounts and aerial photographs taken in the 1940s) (see also Gómez, 1986), 4) higher populations and agricultural activities at the base of the peninsula (from the town of Nicoya north) in comparison to the tip of the peninsula, and 5) rapid deforestation throughout the peninsula during the late 1940s through to the present time.

Cabo Blanco Area. The area now encompassed within the Reserva Natural Absoluta Cabo Blanco has a history that is consistent with what is known of the rest of the peninsula. A special consideration of the topography and vegetation of particular sites within the reserve is warranted, however, because these details may help explain our results on the distribution and abundances of bat species.

Estación Biológica San Miguel is located in the San Miguel (western) sector of the reserve, 2 km south of the community of Malpaís, Costa Rica (Fig. 1). The main station building stands approximately 100 m from the high tide line and about 15 m east of the lower reach of the Quebrada San Miguel. The Quebrada San Miguel is a swiftly flowing stream with pools 2 m deep during the rainy season (May–November) (Fig.

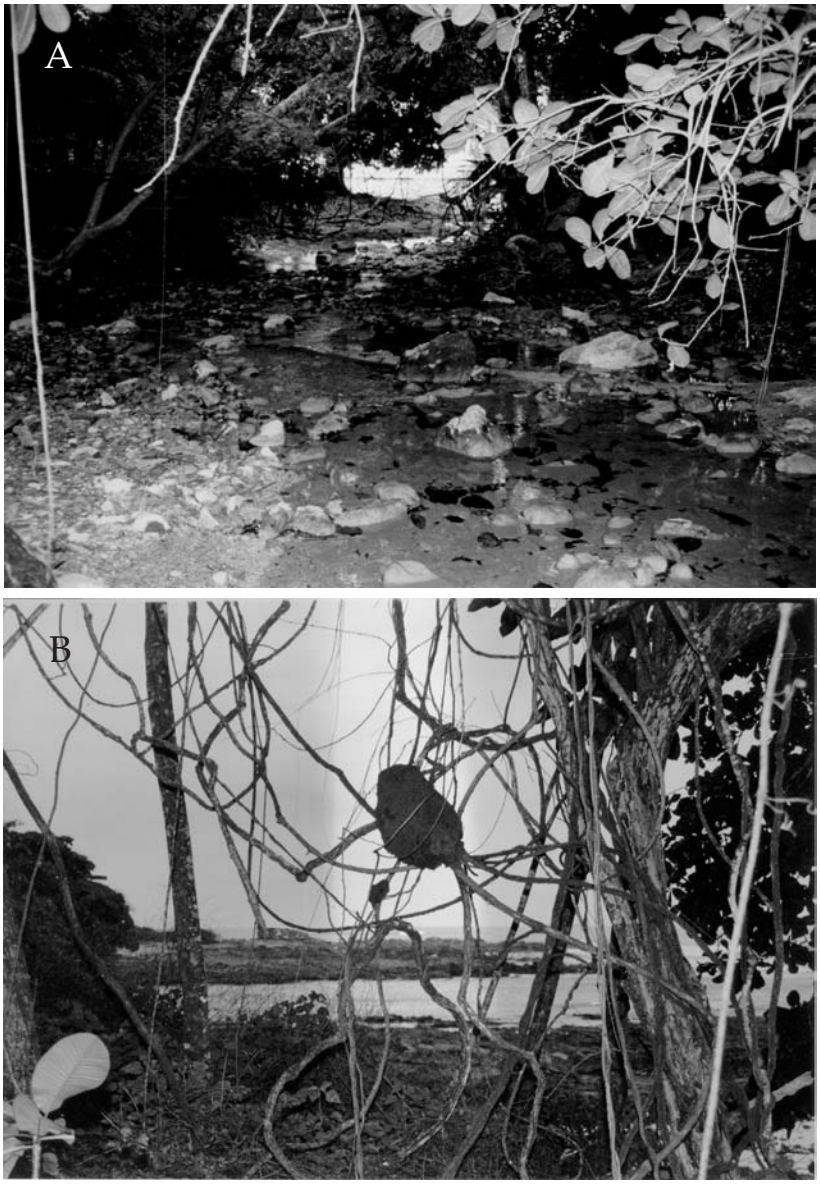

Figure 3. Photographs of 2 sampling sites. (A) Mouth of the Quebrada San Miguel during the rainy season of 2001. The view is from the footbridge next to the station, looking toward the Pacific Ocean. A furled mistnet is in the middle ground, stretched across the stream, in the location where we regularly catch *Noctilio leporinus*. Note the shallow water in the streambed. During the dry season this flow ceases entirely. (B) View of our coastal netting area from the trail where nets were set in the coastal forest (rainy season 2001). In the foreground is a tangle of lianas with a termite (*Nasutitermes*) nest and in the background is the Pacific Ocean looking south toward Isla Cabo Blanco. Photographs by Deedra McClearn.

3A). It dries up seasonally, leaving widely scattered, small and mid-sized pools in its upper reaches and a large pond of brackish water near the ocean. When the rains return, the force of the fresh water in the channel pushes aside the sand deposited by the high tide waves and reopens the way to the sea.

Our coastal forest nets were placed about 50 m from the high tide line, near and across a trail that runs from Quebrada San Miguel to Quebrada Balsitas to the southeast (Fig. 3B). The coastal strip is relatively flat, extends about 3 km in length, and varies in width from 50 to 150 m. Our standard netting positions were southeast of the intermediate, unnamed stream shown on the map. When the reserve was established, this coastal strip was planted in corn, except for a few patches of intact forest (D. Lieberman, pers. comm.). At present, the dominant vegetation along the shoreline includes the native liana *Adenocalymna inundatum* (Bignoniaceae), the fast-growing, native coastal shrub *Taliparitiliaceus* (= *Hibiscus tiliaceus*; Malvaceae), the introduced beach almond *Terminalia catappa* (Combretaceae), and *Plumeria rubra* (Apocynaceae). A few meters inland, the 40 year old regenerating forest is composed of trees such as *Pachira* (= *Bombacopsis* or *Pochota*) *quinata* (Bombacaceae), *Calycophyllum candidissimum* (Rubiaceae), *Cordia collococca* (Boraginaceae), *Hyperbaena tonduzii* (Menispermaceae), *Lonchocarpus felipei* (Fabaceae), *Tabebuia rosea* (Bignoniaceae), *Pseudobombax septenatum* (Bombacaceae), *Sterculia apetala* (Sterculiaceae), and *Bactris major* (Arecaceae). Two of our coastal forest net sites are within a stand of royal palm *Attalea butyracea* (= *Scheelea rostrata*; Arecaceae). The soils here are very sandy and densely occupied by the burrow systems of the land crab *Gecarcinus quadratus* (Gecarcinidae). Hermit crabs (*Coenobita compressus*; Pagaridae) often are so abundant that their nocturnal scratching locomotion can easily be heard over the crash of the nearby surf.

Inland from the coastal strip, the land rises abruptly to a terrace of approximately 70 m elevation. Our inland forest nets were placed over the Quebrada San Miguel and a hiking trail that crosses the stream. Although this location is only a km from our coastal netting station, some of the site characteristics are distinctly different from those along the coast. The ocean cannot be heard from the inland forest netting site, and the density of land crab burrows is much reduced. Some of the tree species are the same as those found closer to the ocean, but inland there are also *Anacardium excelsum* (Anacardiaceae), *Licania arborea* (Chrysobalanaceae), *Manilkara chicle* (Sapotaceae), *Andira inermis* (Papilionaceae), *Brosimum alicastrum* (Moraceae), *Inga vera* (Mimosaceae), and *Luehea seemannii* (Tiliaceae). The understories of both coastal and inland forest have patches of *Piper tuberculatum* and *P. reticulatum* (Piperaceae). Lindquist (2003) and Camacho-Céspedes and Lindquist (in press) provide a broad overview of the trees found in the reserve including descriptions and relative abundances.

The limestone caves (described more fully in the Materials section) are situated in the Refugio de Vida Silvestre Cueva Los Murciélagos, within 200 m of the coast (Fig. 1). It is important to note that continuous forest connects all of the sites where we netted, observed, and handled the bats documented in this paper with the exception of 2 caves. Furthermore, the distances among the sites are within the nightly foraging ranges of most of the species described.

The Bat Fauna

For our results, we use 2 data sets, one of which is a subset of the other. The larger data set includes all of our netting records, cave observations, and incidental observations

Table 1. Bat species inventory for Cabo Blanco, Costa Rica. Total inventory = 39 species. Bats were caught in mist nets (in forest, along coast, or over Quebrada San Miguel), caught by hand (in the caves, in bat tents, and in the dining hall building), observed in limestone caves, observed and photographed in *Attalea* palms, or identified during an Anabat acoustical survey (by Richard K. LaVal, pers. comm.). Some of the forest nets were placed over the upper stretches of the Quebrada San Miguel and some over a hiking trail.

EMBALLONURIDAE
Balantiopteryx plicata (caves; acoustical survey)
Diclidurus albus (seen in *Attalea* along the coast, *N* = 1; acoustical survey)
Peropteryx macrotis (acoustical survey)
Saccopteryx bilineata (caves, flying near central building; acoustical survey)
Saccopteryx leptura (acoustical survey)
MOLOSSIDAE
Eumops (cf. *underwoodi* or *auripendulus*) (acoustical survey)
Molossus ater (acoustical survey)
Molossus molossus (acoustical survey)
Nyctinomops laticaudatus (acoustical survey)
MORMOOPIDAE
Pteronotus parnellii (over stream near mouth, *N* = 1)
NOCTILIONIDAE
Noctilio leporinus (over stream at mouth and over pool in forest; acoustical survey)
PHYLLOSTOMIDAE
Artibeus jamaicensis (coast, forest)
**Artibeus lituratus* (coast only, *N* = 5)
Artibeus phaeotis (coast only, *N* = 1)
**Artibeus watsoni* (coast, forest)
**Carollia castanea* (over stream in forest, *N* = 2)
Carollia perspicillata (coast, forest)
**Choeroniscus godmani* (coast only, *N* = 3)
**Chrotopterus auritus* (coast only, *N* = 1)

Table 1 (continued).

Desmodus rotundus (caves, coast, forest)
Glossophaga soricina (coast, forest)
**Glyphonycteris sylvestris* (forest only, *N* = 1)
Lonchophylla robusta (coast only, *N* = 1)
Lophostoma silvicolum (termite nest in Cabuya sector of Cabo Blanco)
**Micronycteris schmidtorum* (coast only, *N* = 1)
Phyllostomus hastatus (caves, forest)
Platyrrhinus helleri (coast, forest)
Sturnira lilium (coast, forest)
**Sturnira ludovici* (forest only, *N* = 1)
Trachops cirrhosus (forest only, *N* = 8)
Uroderma bilobatum (coast only & roosting under tents in Attalea, *N* = 10 netted)
Vampyrum spectrum (coast only, *N* = 1)
VESPERTILIONIDAE
Eptesicus furinalis (over stream in forest, *N* = 2)
Lasiurus blossevillii (acoustical survey)
Lasiurus ega (forest only, *N* = 5; acoustical survey)
**Myotis elegans* (acoustical survey)
Myotis nigrescens (in dining hall building, coast; acoustical survey)
**Myotis riparius* (forest only, *N* = 2; acoustical survey)
Rhogeessa tumida (coast, forest; acoustical survey)

*First records for Nicoya Peninsula. The determination of new records for the peninsula is based on a combination of criteria including netting records, personal observations, and available range maps.

from 1999 through 2006. The species inventory (Table 1) and the individual species accounts are based on these records. The second data set includes only the netting records from the coastal and inland forest sites during the 4 rainy seasons and 1 dry season for which our times and net placements were standardized. The analyses of netting effort, habitat comparisons, and sex ratios are based on this second data set.

Based on all of our records at Cabo Blanco, we document 39 species of bats belonging to 6 families from 6 years of data (1999–2006) at Reserva Natural Cabo Blanco and adjacent Refugio de Vida Silvestre Cueva Los Murciélagos (Table 1). Twenty-one of the 39 species are in the family Phyllostomidae. Twenty-seven species were captured in mist nets, 5 species of the family Emballonuridae are known from our cave surveys, direct observations, and Anatbat survey, and *Lophostoma silvicolum* from photographs provided by another investigator. Of the 27 species netted, 10 species are known

from only 1 or 2 individuals. Species known from a singleton are: *Pteronotus parnellii*, *Artibeus phaeotis*, *Chrotopterus auritus*, *Lonchophylla robusta*, *Micronycteris schmidtorum*, *Sturnira ludovici*, and *Vampyrum spectrum*. Species known only from 2 individuals are: *Carollia castanea*, *Eptesicus furinalis*, and *Myotis riparius*.

In order to determine whether the rare bats were larger than the more commonly caught bats, we compared the masses of 8 of the 9 singleton individuals (excluding *D. albus*, which we never netted) with the mean mass from all the adult individuals of each of the 10 most commonly caught species (from the habitat comparison data set). There was no significant difference in body mass of the rare and the common bats (Mann–Whitney U-test, $U = 37$, $p = 0.82$).

We ran 1,282.75 m-hours of net in the coastal forest and 499.5 m-hours of net inland. The standardized netting sessions yielded 196 bats from 20 species. Our netting efforts along the coast produced a total of 109 bats with a mean of 0.085 bats per m-hour. Our efforts inland produced a total of 87 bats with a mean of 0.174 bats per m-hour (Table 2). Using a binomial test for the total bats/m h of netting in each habitat, the capture rates were significantly higher inland than along the coast ($p < 0.001$).

The most common bats captured in our inland–coast comparison were *Carollia perspicillata* ($N = 49$), *Artibeus jamaicensis* ($N = 43$), and *Glossophaga soricina* ($N = 20$). *C. perspicillata* accounted for 20% of the bats caught along the coast and 31% of the bats from the inland nets. *A. jamaicensis* accounted for 23% of the coast bats and 21% of the inland bats. There were no significant differences in site of capture for *C. perspicillata* or for *A. jamaicensis*, but *G. soricina* was more likely to be caught in the coastal forest

Table 2. Netting effort and number of bats captured per m-hour along the coast and inland for a 4-year period at Reserva Natural Absoluta Cabo Blanco on the Nicoya Peninsula of northwestern Costa Rica.

	Coast			Inland		
	hours	bats	bats per m-hour	hours	bats	bats per m-hour
July 2000	6.25	18	0.069	5.25	18	0.190
Feb. 2001[1]	4.25	6	0.034	3.50	13	0.155
July 2001	6.00	51	0.200	6.00	24	0.174
July 2002	7.50	18	0.080	5.50	25	0.189
July 2003	8.00	16	0.044	2.50	7	0.156
	Summaries					
Total # of m-hours of net		1,282.75			499.5	
Total # of bats		109			87	
Mean # of bats per m-hour		0.085			0.174*	

[1] dry season

*statistically significant difference in capture rates at the two sites using a binomial test ($p < .001$). We reject the null hypothesis that a captured bat is equally likely to be from a meterhour of netting effort in the inland forest as in the coastal forest.

Table 3. Habitat associations for the eight most commonly netted bats at Reserva Natural Absoluta Cabo Blanco.

Species	*N*	number caught along coast	number caught inland
Carollia perspicillata	49	22	27
Artibeus jamaicensis	43	25	18
Glossophaga soricina	20	19	1*
Artibeus watsoni	15	7	8
Desmodus rotundus	14	7	7
Rhogeessa tumida	12	4	8
Uroderma bilobatum	10	10	0*
Trachops cirrhosus	8	0	8**

Binomial tests for habitat comparisons *$p < 0.001$, **$p < 0.005$
The three indicated comparisons retain significance at an alpha level of 0.05 after a Bonferroni correction for 8 tests.

(19 of 20 captures, binomial test, $p < 0.001$) (Table 3). *Desmodus rotundus* ($N = 14$), *Artibeus watsoni* ($N = 15$), *Rhogeessa tumida* ($N = 12$), *Uroderma bilobatum* ($N = 10$), and *Trachops cirrhosus* ($N = 8$), also were netted in sufficient numbers to permit analysis of habitat associations—there was no significant difference in site of capture for the first 3 species, but *U. bilobatum* was netted only in the coastal forest (10 captures, binomial test, $p < 0.001$) and *T. cirrhosus* only inland (8 captures, binomial test, $p < 0.005$) (Table 3). Habitat associations for *G. soricina*, *U. bilobatum*, and *T. cirrhosus* retain their statistical significance when a Bonferroni correction for 8 tests is applied. Several other species were caught exclusively at 1 of the 2 sites, but sample sizes are not large enough to permit statistical analysis. *Artibeus lituratus* ($N = 5$) and *Choeroniscus godmani* ($N = 3$) were caught only along the coast and *Lasiurus ega* ($N = 5$) only inland.

The sex ratios indicate a predominance of males among our netted individuals. If we consider the collection of bats from species for which we have 10 or more individuals, we reject the null hypothesis of a balanced sex ratio (two-tailed Fisher's Exact test, $N = 142$, $p = 0.036$). For the 2 species with the most male-biased representation, we also reject the null hypothesis of equal numbers of males and females (binomial test for *Uroderma bilobatum*, $N = 10$, $p = 0.021$ and binomial test for *Artibeus jamaicensis*, $N = 32$, $p = 0.043$).

Species observed in the caves included *Balantiopteryx plicata, Saccopteryx bilineata*, *Desmodus rotundus*, and *Phyllostomus hastatus*, all of which are found in the caves year-round (see accounts below). The temperature ranges of all 3 caves are narrow, ranging from approximately 24.0°C near the floor to 26.8°C near the apices.

Sixteen species of bats—*Balantiopteryx plicata*, *Diclidurus albus*, *Peropteryx macrotis*, *Saccopteryx bilineata*, *Saccopteryx leptura*, *Noctilio leporinus*, *Lasiurus blossevillii*, *Lasiurus ega*, *Myotis elegans*, *Myotis nigricans*, *Myotis riparius*, *Rhogeessa tumida*, *Eumops* (cf *underwoodi* or *auripendulus*), *Molossus ater*, *Molossus molossus*, and *Nyctinomops laticaudatus*—were identified by Richard LaVal during his acoustical survey using the Anabat bat-detecting system (LaVal, pers. comm.). Of these, 8 species—*Peropteryx*

macrotis, *Saccopteryx leptura*, *Lasiurus blossevillii*, *Myotis elegans*, *Eumops* sp., *Molossus ater*, *M. molossus*, and *Nyctinomops laticaudatus*—had not been identified previously with mist netting or our other survey methods. The most commonly recorded bat was *Saccopteryx leptura* followed by *S. bilineata*. This is the southernmost record for *Myotis elegans*.

The following section consists of species accounts for every bat that we recorded (excluding those known only from the acoustic survey) from Cabo Blanco. Each account includes a general species distribution, followed by our observations for Cabo Blanco. Information from the nearby Parque National Palo Verde is included as appropriate.

ORDER CHIROPTERA

Family Emballonuridae (Sac-winged Bats)

Balantiopteryx plicata
Gray Sac-winged Bat

The gray sac-winged bat, one of the few Central American bats that occurs primarily in dry forest, is found from western Mexico, along the Pacific basin of Central America, to the Guanacaste lowlands of northwestern Costa Rica, with an isolated population in western Colombia. This species can be very abundant locally, but has a discontinuous distribution.

Balantiopteryx plicata is common in the caves of Refugio de Vida Silvestre Cueva Los Murciélagos at the entrance of the reserve and almost certainly occurs throughout the reserve. We observed this sac-winged bat in 2 or 3 of the caves on each of our visits to the caves in both the rainy season and dry season. This species was observed in all 3 caves, although it was not present in all caves during each visit, suggesting that movement occurs among caves. When a cave was occupied, the numbers varied from 3 to an estimated 155–165 individuals (seen on 4 February 2001 roosting in cave 2). No seasonal or yearly trend is apparent in abundance patterns. On 8 February 2006, we surveyed another limestone cave on private property just to the north of our 3 study caves and located a colony of 150–160 *B. plicata*. It was the only species observed in the cave. *Balantiopteryx plicata* typically roosts near the entrance of caves in groups of 5–10. We have never observed this species roosting in inner, dark areas of caves. An adult female (fa = 43.1; MNCR 178) was collected on 22 April 1994 by Bernal Rodríguez from the caves Refugio de Vida Silvestre Cueva Los Murciélagos. We regularly observe the gray sac-winged bat roosting at Cueva del Tigre in Parque Nacional Palo Verde, during both the rainy and dry seasons.

Diclidurus albus
Northern Ghost Bat

The northern ghost bat is found from Nayarit, Mexico, to eastern Brazil. *Diclidurus albus* generally is considered a rare species throughout its range. Published records for Costa Rica document it as being widely distributed in lowlands, occurring from sea level to perhaps 1,300 m. Richard LaVal (pers. comm.) recently informed us that ghost bats occur at 2,500 m at San Gerardo de Dota. LaVal has recorded the vocalizations of

this species using Anabat software several times in Costa Rica and suggests that it be considered as uncommon but not rare in the country.

We observed a single northern ghost bat at Estación Biológica San Miguel roosting under a frond of the palm *Attalea butyracea* on 4 February 2001. The bat was located ca. 750 m east of the field station roosting ca. 7 m off the ground and hanging from the center of the frond, which was parallel to the ground. This palm was in a grove of mature and immature *Attalea*. We searched this palm grove and others in the vicinity of Estación Biológica San Miguel on subsequent occasions but have never seen another ghost bat.

There is a specimen of *D. albus* in the Museo Nacional de Costa Rica (MNCR 1863) from Playa Montezuma, which is just northeast of the reserve (Rodríguez-H. and Wilson, 1999). We also have observed *D. albus* hanging from a palm frond near the Sirena Biological Station on the Osa Peninsula (Puntarenas Province) and 1 was found in a building at Parque Nacional Palo Verde (Guanacaste Province).

Our observation of *D. albus* at Cabo Blanco and the specimen from Playa Montezuma are the first records for the Nicoya Peninsula, and suggest that this species probably is distributed throughout the peninsula in low numbers.

Saccopteryx bilineata
Greater White-lined Bat

The greater white-lined bat is widespread and occurs from Colima, Mexico, to Brazil. *Saccopteryx bilineata* is common throughout lowland Costa Rica from sea level to 600 m and occurs in both the Pacific and Caribbean lowlands.

Saccopteryx bilineata roosts year-round in the caves of Refugio de Vida Silvestre Cueva Los Murciélagos. We found the greater white-lined bat to use all 3 caves, but it was never found in large numbers in any single cave. Generally, 3–5 *S. bilineata* are seen in each cave. The largest number of individuals observed was 13 on 21 February 2001, when we found 6 individuals in the center cave and 7 in the southernmost cave. *Saccopteryx bilineata* roosts near or at the entrance of caves where it is bright during the day. When both *S. bilineata* and *Balantiopteryx plicata* occur together, *S. bilineata* roosts somewhat interior to *B. plicata*. Both species were observed in all 3 caves, although not necessarily in each cave at each visit, suggesting that movement occurs among caves. *S. bilineata* was present in the largest of the caves (cave 3, the southernmost cave) every time we conducted our cave surveys. We also observed this species roosting along the sides of trees at Cabo Blanco; these colonies are found in dark, shady areas generally several m off the ground, and include 4–5 individuals. At Cabo Blanco, *S. bilineata* can be seen foraging in the clearings beginning a full hour before sunset and in the mornings as late as an hour after sunrise. After extremely heavy rains on the night of 4–5 July 2003, we observed *S. bilineata* foraging throughout the morning hours of 5 July.

Family Mormoopidae (Leaf-chinned Bats)

Pteronotus parnellii
Common Mustached Bat

The common mustached bat is known from Sonora, Mexico, to Brazil across a broad

elevation range from sea level up to 3,000 m and in a wide array of habitats. *Pteronotus parnellii* is common and widely distributed in Costa Rican forests (Timm et al., 1989).

A single adult female (fa = 63, 21 g) *P. parnellii* captured at Cabo Blanco in early February 2000 at 2100 h evinced no sign of reproductive activity. The apparent rarity of mustached bats at Cabo Blanco (ca. 0.33% of our captures) is noteworthy given its abundance at others sites in the Pacific lowlands.

Family Noctilionidae (Bulldog or Fishing Bats)

Noctilio leporinus
Greater Bulldog Bat

The greater bulldog bat is known from Sinaloa and Veracruz, Mexico, to Argentina and throughout the Greater and Lesser Antilles. In Costa Rica, *Noctilio leporinus* is locally common along the coasts, estuaries, and lowland rivers where suitable calm water for fishing exists.

We netted *Noctilio leporinus* throughout the year at San Miguel. Bulldog bats fly conspicuously during both the rainy season and dry season at the mouth of Quebrada San Miguel, where the stream flows into the ocean. We capture the greater bulldog bat regularly (both rainy and dry seasons) near the mouth of the stream. During the rainy season, we have not captured fishing bats further upstream; however, in late dry season (11 April 2003) we captured a nonreproductive adult female over the largest of the pools that remained in the Quebrada San Miguel at 2130 h. Two adult females captured near the mouth of the stream on 2 February 2000 had enlarged teats, and 1 captured on 6 February 2006 was near term.

Family Phyllostomidae (Leaf-nosed Bats)

Artibeus jamaicensis
Jamaican Fruit-eating Bat

The Jamaican fruit-eating bat ranges from Sinaloa and Tamaulipas, Mexico, south through northern South America to Brazil and Paraguay. *Artibeus jamaicensis* is perhaps the most abundant bat at lower elevations throughout Costa Rica and Central America and occupies a wide array of habitats from sea level to at least 1,700 m.

Artibeus jamaicensis is abundant at Cabo Blanco. We captured 49 individuals at Cabo Blanco, including 29 males and 14 females during the rainy seasons (combined), when most of our captures occurred. Twenty were captured inland and 23 along the coast suggesting that this species is not restricted to a specific habitat. We netted this species throughout the evening hours from shortly after sunset until midnight. Forearms of adult females range from 54 to 60 ($\bar{x}$ = 51.8, N = 9); forearms of adult males range from 55 to 69 ($\bar{x}$ = 62.0, N = 21).

We never caught an obviously pregnant female, but 6 of the 7 females captured during July 2001 had an open, blood-infused vulva, suggesting that breeding was ongoing at that time. Fully scrotal males were netted in the dry season (early February 2000 and 4 February 2001) and during the rainy season (17 and 18 July 2000, 17 July 2001, 22 July 2002, and 2 July 2003). Volant juveniles were captured on 17 July 2001.

Artibeus lituratus
Big Fruit-eating Bat

The big fruit-eating bat ranges from Sinaloa, Mexico, through Central America to Argentina. *Artibeus lituratus* is widespread in Costa Rica (from sea level to perhaps 1,500 m) and often is locally abundant, but less so than *A. jamaicensis* at most sites.

We captured 5 *A. lituratus* at Cabo Blanco, all during the rainy season, and all in the coastal forest. On 17 July 2001, we caught a nonreproductive adult female (fa = 68) at 2215 h. On 18 July 2001, we caught an adult male (fa = 68) at 0010 h with enlarged testes. On 2–3 July 2003, we netted 3 male *A. lituratus*—a subadult male with small testes at 1935 h and 2 moderately scrotal adult males at 2015 h. These are the first records of *A. lituratus* for the Nicoya Peninsula.

Artibeus phaeotis
Pygmy Fruit-eating Bat

Pygmy fruit-eating bats occur from Sinaloa and Veracruz, Mexico, through Central America to Ecuador and Guyana. In Costa Rica, *Artibeus phaeotis* ranges from sea level to 1,200 m, but generally is more common at lower elevations and in wetter parts of the country; it may be uncommon or absent in drier areas.

A single adult male (KU 158312) *A. phaeotis* was netted in the coastal forest near Estación Biológica San Miguel on 18 July 1999 by McClearn and C. M. McCain.

Artibeus watsoni
Thomas's Fruit-eating Bat

Thomas's fruit-eating bat is found from Oaxaca and Veracruz, Mexico, through Central America to Colombia. In Costa Rica, *Artibeus watsoni* occurs from sea level to 1,500 m, but generally is more common at lower elevations and in wetter parts of the country and may be uncommon or absent in drier areas.

Our identification of the small *Artibeus* we captured at Cabo Blanco is based upon the size and shape of the talonid of the first upper molar (M1) and presence or absence of the minute last lower molar (m3). We consider the size and shape of the talonid on M1 the most definitive character for the identification of these 2 similar species. The M1 in *A. watsoni* has a small talonid, whereas in *A. phaeotis* the talonid is large and expanded lingually as illustrated in Timm (1985). The minute m3 is never present in *A. phaeotis*. In *A. watsoni* however, this character is variable; some individuals have this minute molar present on both mandibles, some have it present on 1 mandible and not the other, and some lack it entirely. With a single exception (see previous account), all small *Artibeus* that we examined at Cabo Blanco were clearly identified as *A. watsoni*.

Artibeus watsoni is abundant at Cabo Blanco in the dry seasons of 2000 and 2001 and the rainy season of 2001, but was uncommon during our other netting sessions. Eight were captured inland and 7 along the coast, suggesting that this species is not restricted to a specific habitat. Pregnant females and males with enlarged testes were found only during the dry season. Dry season captures included 7 individuals on 2–6 February 2000. One adult female (1840 h, fa = 39) was pregnant and 2 (2300 h, fa = 38; 0005 h, 37) had no obvious signs of reproductive activity. Two adult males (2309 h, fa = 36; fa = 37) had enlarged testes, 1 (0005 h, fa = 35) had intermediate sized testes, and 1

(2240 h, fa = 37) had small testes. Seven individuals were captured on 4 February 2001, including 2 pregnant females (1900 h, fa = 38; 2230 h, fa = 37), 1 adult female (2010 h, fa = 38) that was not obviously pregnant, 2 adult males (1930 h, fa = 36; 2200 h, fa = 36) with enlarged testes, and 2 subadult males (1850 h, fa = 34; 1930 h, fa = 36; 2050 h, fa = 36) with small testes.

Our few rainy season captures included a fully volant juvenile/subadult male (2215 h, fa = 38) with unfused epiphyses captured on 16 July 2001. On 17 July 2001, we captured 2 adult females (1850 h, fa = 39; 2040 h, fa = 38) that had open vaginal orifices, 1 subadult female (1850 h, fa = 34) that evidenced no sign of reproductive activity, and 1 subadult male (1850 h, fa = 34) with small testes. On 22 July 2002, a nonreproductive adult female (2005 h, fa = 38) was observed. On 4 July 2003, we captured 2 adult females (2015 h, 2145 h), neither of which showed signs of recent reproductive activity.

We located 3 tents of *A. watsoni* in *Sterculia apetala*. One tent was occupied by a single adult female *A. watsoni*. All tents were cut with the J-shaped pattern typical of tents made by *A. watsoni* (Timm, 1987). All were in young 3–4 m *S. apetala*, in leaves that hung parallel to the ground and ca. 2 m high. One plant had 2 tents and a second plant a few meters away had a single tent. Our search for tents of *A. watsoni* then and in all subsequent visits to Cabo Blanco failed to locate additional tents. This is the first record of *A. watsoni* using *S. apetala* for tent construction.

These are the first records of *A. watsoni* from the Nicoya Peninsula.

Carollia castanea
Chestnut Short-tailed Bat

Carollia castanea is found from Honduras to Bolivia. LaVal and Rodríguez-H. (2002) reported that in Costa Rica it is common in lowland wet areas on both sides of the continental divide but is rare in the dry Pacific lowlands. It is most common from sea level to 500 m, but has been captured as high as 1,350 m at Monteverde. In intact lowland wet forests, *C. castanea* is more abundant than its congeners, but it also occurs in second growth habitats.

We captured 2 adult *C. castanea* at Cabo Blanco. We captured an adult male on 11 April 2003 in a net set over an isolated spring-fed water hole in the streambed of the Quebrada San Miguel, and a second adult male (10 g; fa = 42) on 5 July 2003 in a net set over the Quebrada San Miguel while it was in full flow. These are the first records of *C. castanea* for the Nicoya Peninsula.

Carollia perspicillata
Seba's Short-tailed Bat

Seba's short-tailed bat is distributed from Puebla, Mexico, to Paraguay. It is an abundant species throughout Costa Rica and Central America and occurs in a wide array of habitats from sea level to at least 1,000 m.

We captured 54 *Carollia perspicillata* at Cabo Blanco. During our paired netting efforts, 27 were captured inland and 22 along the coast; additional individuals were netted in a variety of habitats. This species is the most abundant bat we captured during the rainy season, but is uncommon during the dry season. Forearms of adult females range from 41 to 45 ($\bar{x}$ = 42.4, N = 22); forearms of adult males range from

40 to 44 ($\bar{x}$ = 42.3, N = 17). We captured this species throughout the evening from shortly after sundown through our final netting for the evening, which generally was after midnight. *Carollia perspicillata* often was one of the earliest species captured each evening. Captures were most abundant from shortly after sundown and dropped off in the late evening.

Reproductive activity occurred in both the dry and rainy seasons. During the dry season, we have evidence for male reproductive activity—5 adult males, all of which were fully scrotal, on 2–6 February 2000 and a single adult male (fa = 40) with enlarged testes on 4 February 2001. Although males had large testes during the dry season, we never caught a female that was obviously pregnant or receptive. During the rainy season, we observed different states of reproductive activity in both males and females. On 17–20, July 2000 short-tailed bats, including a single adult male that was fully scrotal and 5 adult females, none of which was obviously pregnant, were captured. On 16–18 July 2001, we netted 6 adult males, 11 adult females, 3 juvenile males, and 1 juvenile female. Two of the males were fully scrotal, 2 of the females were pregnant, and 8 females had open vulvas. On 20–22 July 2002, we caught 9 males and 8 females; 4 of the males and 2 of the females were judged to be young adults. Of 2 males and 1 female captured on 4–5 July 2003, 1 male was fully scrotal, 1 male was moderately scrotal, and the female evidenced no sign of reproductive activity. An adult female (fa = 42.2; KU 158316) was collected near Estación Biológica San Miguel on 18 July 1999 by McClearn and McCain.

At Cabo Blanco we have not observed the similar appearing *C. subrufa*, a species that makes up a regular, albeit small, percentage of our captures at Palo Verde, nor have we observed *C. sowelli*, which may be abundant at higher elevations in Costa Rica.

Choeroniscus godmani
Godman's Whiskered Bat

Godman's whiskered bat is known from a poorly understood, discontinuous range from Sinaloa, Mexico, to Colombia, Venezuela, and Suriname. In Costa Rica, *Choeroniscus godmani* is found from sea level to 1,500 m, but is seldom encountered and little is known of its biology.

We captured this nectar-feeding bat on 3 occasions at Cabo Blanco, all along the coast and during the rainy season. A pregnant adult female (fa = 37.6) was captured on 17 July 2000 at 1830 h. Two females, which showed no recent reproductive activity, were captured on 22 July 2002, 1 adult (fa = 37) at 1830 h and 1 young adult (fa = 37) at 2145 h. These are the first records of *C. godmani* from the Nicoya Peninsula.

Chrotopterus auritus
Woolly False Vampire Bat

The woolly false vampire bat occurs from the southern Mexican states of Oaxaca and Veracruz through Central America to the Guianas, across northern and southern Brazil and eastern Peru, to northern Argentina. Although *Chrotopterus auritus* is widely distributed, few specimens of this species exist and little is known of its distribution and biology. As with all of the predaceous phyllostomids, this species generally is

considered to be highly vulnerable to human disturbance.

We netted a single adult male *C. auritus* (fa = 84) in the coastal forest on 17 July 2001 at 2235 h. Although the woolly false vampire bat is a cave-roosting species, we have not observed it in Refugio de Vida Silvestre Cueva Los Murciélagos. The adult male is the first observation of the species on the Nicoya Peninsula and this record is especially noteworthy because forests in the reserve and throughout the Nicoya Peninsula have been heavily impacted by clearing for agriculture.

We regularly observe a small colony of *C. auritus* roosting in Cueva del Tigre in Parque Nacional Palo Verde during both the rainy season and dry season. These bats roost high in the cave, and the individuals cluster tightly together. We have found beetle elytra and cockroach (*Blaberus giganteus*) wings beneath these diurnal roosts.

Desmodus rotundus
Common Vampire Bat, Vampiro

The common vampire bat occurs from Sonora and Tamaulipas, Mexico, to Argentina. In Costa Rica, *Desmodus rotundus* is found from sea level to 2,700 m, and may be locally abundant, especially where there are cattle. However, vampires are uncommon or rare in larger blocks of intact forest where domesticated livestock are not present.

Desmodus rotundus is common at Cabo Blanco, and we captured this species during nearly every netting session. Twelve individuals were captured on the nights of 16–17 July 2001 in our nets in the reserve, although other netting efforts took smaller numbers. In the caves at Refugio de Vida Silvestre Cueva Los Murciélagos, we observed colonies of *D. rotundus* each time we visited, documenting that they are residents in the caves throughout the year. All 3 caves contained roosting colonies of vampires on most, but not all of our visits. The northernmost cave generally had the largest population, estimated at 20–25 individuals in February 2001 and 100 in July 2001, and was occupied each time we visited. Smaller numbers, ranging from just a few to 30, were found in the other 2 caves. Adult females with nonvolant young were observed in early and mid-February, mid-April, and early and mid-July in different years. Young vampires of different ages were seen with the adults during both the rainy season and dry season, documenting that reproduction occurs year-round. We attribute the seasonal and yearly differences in numbers of vampires in the caves to movement among the caves, and perhaps to movement to other caves in the region. The temperature ranges of roosting sites ranged from 25.4 to 26.2°C and vampires are found in dark areas, both in crevices and on flat expanses of walls.

The caves are located between the reserve and the community of Malpaís. We suspect that vampires here feed primarily on cattle from the adjacent farms, and we were told that vampires frequently do feed on cattle in the area. In the reserve, we netted *D. rotundus* early in the evening along the coast as they were heading towards the ocean. It is possible that these individuals feed on roosting sea birds on nearby Isla Cabo Blanco.

Within the reserve at Cabo Blanco, we captured an adult female (2250 h, fa = 62) in early February 2000 that was not obviously pregnant. On the nights of 16 and 17 July 2001, we captured 12 individuals including 11 adults and 1 juvenile. Adult females included 3 (1940 h, fa = 62; 2050 h, fa = 63; 2132 h, fa = 60) with an open blood-infused vulva and 1 (1930 h, fa = 59) that was not reproductively active. Adult males captured include 3 (1940 h, fa = 58; 2130 h, fa = 58; 2140 h, fa = 59) that were moderately scrotal

and 2 (1940 h, fa = 58; 2314 h, fa = 58) that had small testes.

Glossophaga soricina
Common Long-tongued Bat

The common long-tongued bat is distributed from Sonora, Mexico, to northern Argentina. In Costa Rica, *Glossophaga soricina* occurs from sea level to 1,500 m. It is an abundant species throughout Central America, especially in disturbed habitats.

Glossophaga soricina is a common species at Cabo Blanco during the rainy season and along the coast; 19 of 20 *G. soricina* were caught along the coast. The ratio of 18 sexed animals was heavily biased toward males—14 adult males and 4 adult females. Our captures were distributed throughout the evening hours until 2330 h. Forearms of adult females ranged from 36 to 38 ($\bar{x}$ = 37.0, N = 4); forearms of adult males ranged from 35 to 38 ($\bar{x}$ = 36.3, N = 14).

Our evidence indicates that males may have enlarged testes during both the rainy and dry seasons, but we only captured pregnant females in the dry season. In early February 2000, 3 adult females were captured; 2 were pregnant (1910 h, 1935 h) and 1 not obviously pregnant (2000 h). On 3 February 2001, 1 scrotal adult male (1855 h) was captured. During the rainy season, when we had most of our *G. soricina* captures, scrotal males were observed but no female was obviously pregnant. On 17 July 2000, we captured 10 adults, 4 females and 6 males—none of the females (1910 h, 2305 h, 2325 h, 0014 h) were obviously pregnant, 5 males (1845 h, 1840 h, 1840 h, 1903 h, 2225 h) were fully scrotal and 1 (2100 h) had small testes. On 17 July 2001, we captured 1 adult female (1945 h) with no evidence of reproductive activity and 4 males, 2 fully scrotal adults (1850 h, 1915 h) and 1 juvenile male (1850 h) with small testes. On 4 July 2003, an adult male (1840 h) was captured with small testes.

A single specimen of *G. soricina* from nearby Tambor is in the collection at the University of Michigan (UMMZ 65096).

Glyphonycteris sylvestris
Tricolored Bat

The tricolored bat ranges from Nayarit and Veracruz, Mexico, south to Peru and southeastern Brazil, and is primarily a low elevation species (below 800 m). It is rare throughout this broad geographic range. We follow recent phylogenetic studies that refer this species to *Glyphonycteris* rather than *Micronycteris* (as it has been treated historically) because the traditionally recognized genus was paraphyletic (Wetterer et al., 2000). LaVal and Rodríguez-H. (2002) reported that this species is uncommon in the Guanacaste and northern Caribbean lowlands of Costa Rica. We caught a single adult male *G. sylvestris* (fa = 39) at 1900 h on 20 July 2002 in a net set across the Quebrada San Miguel in the inland forest at Estación Biológica San Miguel.

Lonchophylla robusta
Panama Long-tongued Bat

The Panama long-tongued bat is an uncommon species that occurs from southeastern Nicaragua to Peru and Venezuela. In Costa Rica, *Lonchophylla robusta* is known from

only a few localities from sea level to 1,000–1,500 m (LaVal and Rodríguez-H., 2002).

We caught a single adult female *L. robusta* (fa = 39) at Cabo Blanco along the coast at 1840 on 16 July 2000. She was not obviously pregnant. This is the first record of this species for the Nicoya Peninsula.

Lophostoma silvicolum
White-throated Round-eared Bat

The white-throated round-eared bat is an uncommon species found in lowland forests from southern Honduras to Bolivia and northeastern Argentina. *Lophostoma silvicolum* has been observed in Costa Rica only a few times; it is known from both the Caribbean and Pacific lowlands at elevations below 500 m.

Two *L. silvicolum* were observed roosting in a cavity in an arboreal termite nest in the eastern sector of Reserva Natural Absoluta Cabo Blanco in July 2002. Alex Mordas observed and photographed the round-eared bats roosting in a cavity that ran along the length of the nest and perpendicular to the ground. Although the bats were not handled at the time, we are confident that they were *L. silvicolum* based on our study of the photographs. We identified the bat as *L. silvicolum* rather than *L. brasiliense* or *Tonatia saurophila* because of the very large, rounded ears that are joined at the base and haired at the inner edge; the overall gray coloration dorsally and the sharp contrast between the darker dorsal coloration and the white fur of the ventral neck region; the long, somewhat woolly fur; the pale stripe between the eyes; and the lightly haired face with a small noseleaf. We follow a recent molecular systematics revision of the genus *Tonatia* in treating the genus as paraphyletic with a distinct lineage referable to *Lophostoma*, which includes the species *L. brasiliense*, *L. carrikeri*, *L. evotis*, *L. schulzi*, and *L. silvicolum* (Lee et al., 2002).

Termites of the genus *Nasutitermes* (Isoptera: Termitidae) are moderately common at Cabo Blanco and make characteristic nests from 1 to several meters off the ground on the trunks of trees. During each of our visits to the western sector, we searched termite nests for excavated cavities and roosting bats, but with no success.

Three species of *Lophostoma* (*L. brasiliense*, *L. carrikeri*, and *T. silvicolum*) are known to use these large, waterproof termitaria as diurnal roosting sites (Kalko et al., 1999). *L. silvicolum* was expected to occur on the Nicoya Peninsula, although there are no previous records.

Micronycteris schmidtorum
Schmidt's Big-eared Bat

Schmidt's big-eared bat is found from southeastern Mexico through Central America to northeastern Brazil and Peru. *Micronycteris schmidtorum*, a rare and poorly known phyllostomine throughout its range, is known from Costa Rica by only a few specimens. The few captures of this species are all from the lowlands and include both the Pacific and Caribbean coasts.

An adult male (7.5 g; fa = 34.0; KU 158317) was collected in the coastal forest on 18 July 1999 by McClearn and McCain. This is the first record of *M. schmidtorum* from the Nicoya Peninsula.

Phyllostomus hastatus
Greater Spear-nosed Bat

The greater spear-nosed bat occurs from Belize and Honduras to Brazil and northern Argentina. *Phyllostomus hastatus* is the most abundant of the large, carnivorous bats in Central America and in Costa Rica is found from sea level to 1,000 m.

We found colonies of spear-nosed bats roosting in the southernmost cave (cave 3) at Refugio de Vida Silvestre Cueva Los Murciélagos on each of our 8 visits there, during both the rainy season and dry season. The colony size was estimated at >70 individuals on 2 occasions (1 dry season and 1 rainy season) and at 35–40 on 2 occasions (rainy season). This is the darkest of the caves and has the largest, most topographically complex ceiling. It is the only cave to consistently have a colony of spear-nosed bats. The spear-nosed bats most frequently hung in extremely tight clusters from the ceiling where it was generally 4 m high or higher. The bats tended to roost in avons (a small eroded pocket in the ceiling of a cave) or other cavities in the ceiling. On some of our visits we also observed individuals roosting singly. A small colony of *P. hastatus* (5–10 individuals) was observed in cave 1 on 2 occasions.

We captured a single adult female in a net set in the inland forest on 20 July 2000. She was not obviously pregnant. On 23 July 2002, Timm watched an adult hanging from the ceiling of cave 3 capture and consume an adult *Polistes erythrocephalus* (Hymenoptera: Vespidae). The bat was hanging adjacent to an occupied wasp nest when first seen. The bat grabbed the wasp from the surface of the nest with its teeth and quickly chewed and consumed the insect.

A volant subadult male *Phyllostomus hastatus* (fa = 85, 84 g; MNCR 175) was collected at Cabo Blanco on 21 April 1994 by Bernal Rodríguez.

Platyrrhinus helleri
Heller's Broad-nosed Bat

Heller's broad-nosed bat occurs from Oaxaca and Veracruz, Mexico, to central Brazil. In Costa Rica, *Platyrrhinus helleri* is a lowland species found on both coasts from sea level to perhaps 1,500 m and generally is not an abundant species.

On 5 July 2003, we caught 4 adult *P. helleri*, 2 males and 2 females, in the inland forest in a net set over the Quebrada San Miguel. Neither of the females was obviously pregnant or showed any other evidence of recent reproductive activity. The males were not obviously scrotal. No other *P. helleri* were captured during our rainy season–dry season comparisons. On 11 April 2003 in the late dry season, we captured 15 adults in one-half hour in 2 nets set over isolated pools in the Quebrada San Miguel. This was the most abundant species we captured that evening. Richard LaVal informed us that he captured and released an adult female carrying a near-term embryo in late February 2005 in a net set over the Quebrada San Miguel near the field station. *Platyrrhinus helleri* was reported previously from Cabo Blanco by Rodríguez-H. and Wilson (1999) on the basis of a young adult female (fa = 38.4, 13 g; MNCR 169) collected on 19 April 1994.

Sturnira lilium
Yellow-shouldered Bat

The yellow-shouldered bat is known from Sonora and Tamaulipas, Mexico, to Argentina. *Sturnira lilium* is widespread through Costa Rica's lowlands and has been taken as high as 1,500 m. This species usually is more abundant in dry forest than in wet forest, and often is one of the most commonly captured species at a site. The similarity between this and related members of the genus (including at least 1 undescribed species; Timm unpubl.) from the southern Pacific region of Costa Rica makes accurate determination of species ranges problematic (Timm and Rodríguez, in prep.).

Over 3 rainy seasons, we captured 8 adult *S. lilium* at Cabo Blanco—4 inland and 4 along the coast. Our data suggest reproduction in early but not late July; since these records are not all from the same year, however, this pattern is merely suggestive. Two pregnant females were netted on 5 July 2003, 1 at 1833 h (fa = 37) and 1 at 1850 h (fa = 39), and a third female (fa = 37) at 1927 h had enlarged teats and was lactating. On 17 July 2001, an adult female (fa = 39) had an open pubic symphysis. Females with no apparent recent reproductive activity were caught on 17 July 2000 (fa = 37) at 1934 h and on 20 July at 1845 (fa = 37) and 2315 (fa = 41). On 18 July 2000 (fa = 39) at 1905 h, a nonscrotal adult male was captured over Quebrada San Miguel. An adult male *S. lilium* (MNCR 164) was collected at Cabo Blanco on 18 April 1994 by Bernal Rodríguez.

Sturnira ludovici
Highland Yellow-shouldered Bat

The highland yellow-shouldered bat is widely distributed from Sinaloa and Tamaulipas, Mexico, to Peru and Bolivia. This species occurs from sea level to high elevations in Costa Rica, but is most common at middle elevations.

We captured a single young adult male (fa = 39) *Sturnira ludovici* at Cabo Blanco on 20 July 2002 at 2110 h in the inland forest. This male had nearly fused wing epiphyses and sharp, unworn teeth. He did not have enlarged testes. This is the first record of *S. ludovici* for the Nicoya Peninsula.

Trachops cirrhosus
Fringe-lipped Bat

The fringe-lipped or frog-eating bat is found from Oaxaca and Veracruz, Mexico, to Brazil. *Trachops cirrhosus* is found throughout Costa Rica from sea level to 1,550 m.

At Cabo Blanco, we caught fringe-lipped bats regularly in nets set across the trail at our inland site and around isolated pools in Quebrada San Miguel during the dry season. We have never taken this species in nets across the stream during the rainy season when it was flowing or along the coast. A net set across a trail on the inland ridge captured *T. cirrhosus* each time we netted there during both the rainy season and dry season over the 4-year period. One pregnant adult female (fa = 59) was captured on 16 July 2001 at 1945 h. Two adult females handled on 18 July 2000 at 1850 h (fa = 58) and at 2210 h (fa = 61) and on 4 February 2001 at 1915 h (fa = 59) evidenced no obvious signs of reproductive activity. Three adult males captured included 1 that was fully scrotal on 18 July 2000 at 2050 h (fa = 59), 1 that was moderately scrotal on 16 July 2001

at 1945 h (fa = 57), and 1 with small testes on 4 February at 1915 h (fa = 58).

On 11 April 2003, we found a number of fringe-lipped bats actively circling over the Quebrada San Miguel beginning an hour after sunset. The streambed was dry except for isolated pools. When frogs (*Eleutherodactylus*) began calling well after sundown, the fringe-lipped bats became active, swooping back and forth in the region where the male frogs called.

Uroderma bilobatum
Common Tent-making Bat

The common tent-making bat is found from Oaxaca and Veracruz, Mexico, to Brazil. *Uroderma bilobatum* occurs in a wide array of habitats ranging from primary humid and dry forests to second-growth and pastureland. This is a common species in Costa Rica and is found from sea level to 1,200 m.

As the common name implies, *U. bilobatum* constructs roosts by modifying large leaves to form a tent for use as diurnal roosts and maternity sites. At Cabo Blanco, tents of *U. bilobatum* are abundant in the palm *Attalea butyracea* and were found in this palm during each of our visits. *Uroderma bilobatum* makes an elongate inverted V-shaped tent in *A. butyracea* by cutting the leaflets extending out from the midrib in a manner similar to that described for other species of pinnately compound-leafed palms (Timm, 1987; Timm and Lewis, 1991). This bat has a harem mating system with roosting groups including a single adult breeding male, a number of adult females, and their associated young. During each of the rainy seasons, we found several groups of *U. bilobatum* roosting under the tents and other individuals roosting singly. These clusters included lactating females with young and males with enlarged testes. During the dry season, we only observed *U. bilobatum* roosting singly and very few (1–3) bats were present under the tents in any year. We found tents of *U. bilobatum* only in *A. butyracea* at Cabo Blanco despite the wide array of plant species known to be used by this species for tents in other areas.

Based on tent surveys and netting data, both males and females are abundant at Cabo Blanco along the coast during the rainy season. Both sexes are far less abundant during the dry season. No tents were located away from the coast and we never netted this species away from the coast. Rainy season captures during our habitat surveys consisted of 6 adult males and 1 female. Of 2 adult males from 17 July 2000, 1 (1845 h, fa = 39) was fully scrotal and 1 (1945 h, fa = 43) was moderately scrotal. On 17 July 2001, we captured a single adult male (fa = 40) at 1915 h. On 22 July 2002, we captured 2 adult males (1830 h, fa = 46; 2105 h, fa = 42). On 5 July 2003 a moderately scrotal adult male was netted at 1945 h. The single female we netting was a nonreproductive adult on 5 July 2003 (fa = 42). Our dry season records include 3 adult males (1840 h, fa = 41; 1850 h, fa = 44 h; 2225 h, fa = 44), all with enlarged testes, and a single adult female (1850 h, fa = 43) that was not reproductively active on 3 February 2001.

Vampyrum spectrum
Great False Vampire Bat

The false vampire bat ranges from Veracruz, Mexico, to southwestern Brazil. In Central America, the species is found from sea level to at least 1,650 m (Reid, 1997). *Vampyrum spectrum* is a rare bat throughout its range and also is rare in Costa Rica, where it is

known from only a few localities.

We captured a single young adult female *V. spectrum* (fa = 104) in the coastal forest at 0010 h on 17 July 2001. Her teats were minute and the vaginal orifice small and lacking pigment or other evidence of reproductive activity and we judged her to be nulliparous. This large predaceous bat flew into a net within 0.5 m of where we were extracting a distressed and vocalizing *Artibeus*. This is the first record of *V. spectrum* from the Nicoya Peninsula.

Family Vespertilionidae (Evening Bats)

Eptesicus furinalis
Argentine Brown Bat

The Argentine brown bat ranges from Jalisco and Tamaulipas, Mexico, south to Argentina. *Eptesicus furinalis* occurs in a wide range of environmental conditions from sea level to middle elevations, although it is not common in Costa Rica.

We captured 2 *E. furinalis* at Cabo Blanco; both were netted over the Quebrada San Miguel. An adult female (fa = 41) was caught in the inland forest on 18 July 2000 at 2005 h. She was not obviously pregnant. An adult male (7 g) was taken on 5 July 2003.

Lasiurus ega
Southern Yellow Bat

The southern yellow bat is found from southeastern Texas and adjacent Mexico to Argentina. This species has an enormous geographic range and occurs in a wide variety of habitats ranging from rainforest to xeric desert scrub. In Costa Rica, *Lasiurus ega* occurs from sea level to montane habitats, but it is not an abundant bat.

We observed *L. ega* on 5 separate occasions at Cabo Blanco during both the rainy season and dry season. Rainy season captures include an adult male (fa = 48) on 16 July 2001 at 2235 h and an adult female (fa = 48) on 20 July 2002 at 2045 h. During the dry season, we captured an adult female (fa = 48) in early February 2000 at 2020 h and another (fa = 42) in early February 2001. None of the females had evidence of recent reproductive activity, and none of the males had obviously enlarged testes. Most were netted over the Quebrada San Miguel. All were captured inland.

Richard LaVal (pers. comm.) informed us that he also has netted *L. ega* at Cabo Blanco. These are the first records of *L. ega* for the Nicoya Peninsula.

Myotis nigricens
Black Myotis

The black myotis is distributed from Tamaulipas, Mexico, to Argentina. It often is an abundant species roosting in buildings throughout Central America. In Costa Rica, *Myotis nigricans* is found from sea level to more than 3,000 m.

Individuals of *M. nigricens* regularly roost in the buildings of Estación Biológica San Miguel both in the rainy and dry seasons. We observed black myotis roosting only as single individuals, and in all cases an individual was seen tightly wedged in a small space between the ceiling planks or between the screens and the ceiling or walls. All

bats were located close to the ceiling. *Myotis nigricens* is the only species of bat we saw roosting in the buildings at Cabo Blanco. This species was reported previously from Cabo Blanco by Rodríguez-H. and Wilson (1999) based upon an adult male (fa = 34.5, 3 g; MNCR 184) collected in the San Miguel Sector on 20 April 1994.

Myotis riparius
Riparian Myotis

The riparian myotis is known to occur from Honduras to Uruguay. It occupies a wide elevational range and wide array of habitats including both forested and savannah regions. In Costa Rica, *Myotis riparius* is known from sea level to at least 2,000 m (LaVal and Rodríguez-H., 2002).

We obtained *M. riparius* during both the rainy and dry seasons. An adult female (fa = 34) was captured on 18 July 2000 at 1835 h, and during the dry season, an adult female (fa = 33) was captured in early February 2000 at 2040 h. Neither female evinced sign of reproductive activity. These are the first records of *M. riparius* for the Nicoya Peninsula.

Rhogeessa tumida
Central American Yellow Bat

Rhogeessa tumida is the name applied previously to yellow bats occurring from eastern Mexico to northern South America; however, recent cytogenetic studies demonstrate that the genus is more speciose than previously believed and several biological species are represented in this broad geographic range. Genoways and Baker (1996) suggested that 10 species be recognized in the genus, with 2 (*R. tumida* and *R. io*) occurring in Costa Rica and Nicaragua. They considered the populations in Costa Rica's northwestern Pacific lowlands to be *R. tumida* and the species that occurs in the Caribbean lowlands and on the Osa Peninsula to be *R. io*, although they lacked specimens from those regions for cytogenetic studies. When studying specimens from Costa Rica, Timm and LaVal (1998) found *R. tumida* to be significantly smaller in size and lighter in color than *R. io*, and suggested that all *Rhogeessa* in the northwestern lowlands would be *R. tumida*. Based on forearm measurements, which range from 29 to 34 mm, and their lighter color, we assign the yellow bats of the southern Nicoya Peninsula to *R. tumida*. LaVal and Rodríguez-H. (2002) considered *R. tumida* to be an uncommon lowland species in the dry forests of Guanacaste, where it occurs up to 850 m. Timm et al. (1999) provided a more detailed review of the taxonomic history of Costa Rican *Rhogeessa*.

The yellow bat is encountered regularly at Cabo Blanco, especially in nets set over the Quebrada San Miguel, although not in high numbers. *Rhogeessa tumida* is one of the earliest bats caught in the evening. Eight were captured inland and 4 along the coast; in light of the fact that we had half the netting effort inland as along the coast, these observations suggest that this species is more abundant inland than along the coast. Most were captured in nets set over the stream. Adult females were captured on 18 July 2000 at 1855 h (fa = 29), 3 February 2001 at 1819 h (fa = 31), 16 July 2001 at 1813 h (fa = 30), 16 July 2001 at 1830 h (fa = 29), and 17 July 2001 at 2145 h (fa = 33). Adult males were captured on 18 July 2000 at 2145 h (fa = 34), 16 July 2001 at 1830 h (fa = 30), 20 July 2002 at 2305 h (fa = 30), 4 July 2003 at 1820 h (fa = 31), and 5 July 2003 at 1838 h (fa = 29). None of the females were obviously pregnant or had enlarged

nipples. One male captured on 18 July had enlarged testes, and 1 captured on 5 July had moderately enlarged testes.

The only previous records of *R. tumida* from the Nicoya Peninsula are a single adult female (MNCR 183) collected at Cabo Blanco by Bernal Rodríguez and 2 specimens from Sámara (Guanacaste Province) reported by LaVal (1973).

DISCUSSION

For more than 4 decades, Reserva Natural Absoluta Cabo Blanco at the southern tip of the Nicoya Peninsula has been safeguarded from logging, hunting, and agricultural uses. Because human impact has been minimized here in recent years, wildlife has been protected and the forest is regenerating rapidly. Several mid-sized mammals that are uncommon in many areas of Central America are now common at Cabo Blanco. For example, white-faced capuchins (*Cebus capucinus*), tamandua anteaters (*Tamandua mexicana*), and white-nosed coatis (*Nasua narica*) are especially abundant in the reserve, and can be seen on a daily basis. Some poaching of game species does occur, however, as it does throughout the country, and we found the carcasses of 2 white-tailed deer (*Odocoileus virginianus*) that had been shot.

Our bat-netting efforts at Cabo Blanco over a 6-year period were designed as two-day field projects for graduate level tropical ecology courses run by the Organization for Tropical Studies. We present our observations in the species accounts above regarding reproduction and other aspects of natural history. Our data provide several first-capture records for the Nicoya Peninsula and have implications for forest and bat conservation as outlined below. Our capture data are heavily weighted toward the rainy season and our statements about seasonal patterns of bat abundance and reproduction must be considered preliminary. We make several statements regarding microhabitat differences of the bats at Cabo Blanco (in terms of how many bats are caught in a standard unit of netting effort and with regard to which bats are found where), but a more intensive study clearly is needed.

Diversity.—In 16 full evenings of netting, several partial evenings of netting, several cave surveys, targeted search and netting events, and an acoustical survey over 6 years, we identified 39 species of bats representing 6 families as occurring at Cabo Blanco. Phyllostomids accounted for 21 of the 39 species recorded. This dominance of phyllostomids is typical of Neotropical bat communities from Mexico to Paraguay with the total number of species depending on factors such as netting effort (Stevens et al., 2004; Stoner, 2005), size and heterogeneity of the sampling area (Moreno and Halffter, 2000; Gorresen and Willig, 2004), the variety of techniques used to capture bats (Voss and Emmons, 1996), and the latitude of the site (Stevens, 2004). Our survey efforts have not resulted in a complete bat inventory. We did achieve the 18 nights of netting that Moreno and Halffter (2000) considered adequate for identifying approximately 90% of the nettable bat species in a heterogeneous habitat in Mexico, but we are short of the 1,000 captures recommended by Bergallo et al. (2003) for a complete inventory. A concerted year-round bat community study using a variety of techniques would certainly increase the number of bats identified from this region of the Nicoya Peninsula. We expect that additional species of *Pteronotus* and molossids will be found in the reserve. Timm and W. Pineda (unpubl.) document that molossids

are more common and widely distributed in Costa Rica's dry forest than had been previously believed. Of the species recorded, two-thirds (27 of 39) were captured in mist nets and one-third (N = 13) were detected only by other methods. Clearly mist nets are only one of the techniques that should be used in assessing the diversity of bats in the Neotropics.

Singletons.—Nine of the 27 (33.3%) species caught in mist-nets are known from only 1 individual and 3 others from only 2 captures. The rare species in the Cabo Blanco bat community are not larger in mass than the most common species. Although *Vampyrum spectrum* and *Chrotopterus auritus* (only 1 individual netted of each species) are the largest bats in the Neotropics, 3 other singletons were among the 4 smallest bats from the full assemblage, and 2 were mid-sized. This result agrees with a multi-site analysis of Neotropical bat communities (Arita, 1993), but goes against the general mammalian trend for large animals to have smaller population sizes.

Species known from a single individual in biodiversity inventories have several potential roles. Very low local abundance is a component of rarity and, as such, a possible criterion for identification of an endangered species (Arita, 1993). The addition of new rare species over time also could signal a shift in species' ranges and/or gradual climate change. Medellín et al. (2000) considered a large number of singletons in a bat inventory to be a sign of undisturbed forest. For hyperdiverse groups, the supply of singletons may be virtually limitless (i.e., lowland Neotropical ants—Longino and Colwell, 1997; Amazonian spiders—Silva and Coddington, 1996), but one would expect that with less diverse groups such as bats an increase in sampling effort would lead to a reduction in the number of species represented by a lone individual. It is interesting to note that after 56 nights of netting over 3 years at Parque Nacional Palo Verde, 17 of 47 (36%) species of bats were still known from only a single individual (Stoner and Timm, 2004).

Bat Inventories as an Indication of Habitat Disturbance.—The animalivorous bat fauna of Cabo Blanco is of particular interest in that the 3 largest carnivores in the Neotropics (*Chrotopterus auritus*, *Phyllostomus hastatus*, and *Vampyrum spectrum*) are present as are 2 other large predators, *Noctilio leporinus* and *Trachops cirrhosus*. Three of these species are abundant (*N. leporinus*, *P. hastatus*, and *T. cirrhosus*) and 2 are rare (*C. auritus* and *V. spectrum*; both known only by single captures). However, the small and middle-sized predatory bats are poorly represented. We have single observations of *Glyphonycteris sylvestris*, *Micronycteris schmidtorum*, and *Lophostoma silvicolum*), and other small and middle-sized species could be expected to occur in the region.

A number of authors propose using characteristics of a Neotropical bat community (or the phyllostomid subsection of the community) as correlates of the level of habitat disturbance. Indicators of minimal disturbance include the presence of phyllostomines (animalivorous bats) (Fenton et al., 1992; Timm, 1994; Patterson et al., 2003; Gorresen and Willig, 2004), the presence of more large than small fruit eaters (Schulze et al., 2000), and the proportion of rare species (Medellín et al., 2000). Indicators of considerable habitat disturbance include the dominance of 1 particular species (> 34% of total captures) (Medellín et al., 2000) and the prevalence of *Sturnira lilium* and *Carollia perspicillata* (Schulze et al., 2000) and *Desmodus rotundus* (Wilson et al., 1996). It is important to note that these studies were conducted in different sites widely scattered in the Neotropics (Costa Rica, Guatemala, Mexico, Paraguay, Peru) and the disturbed

areas vary from forest fragments to cacao plantations to regenerating secondary forest. By these criteria, Reserva Natural Absoluta Cabo Blanco has characteristics of both a relatively undisturbed habitat and of a disturbed habitat. In the former category are: several species of phyllostomines, few *Sturnira lilium*, a substantial number of large frugivores (*Artibeus jamaicensis*), and several rare species. Possible indicators of habitat disturbance include large numbers of *Carollia perspicillata* and the moderate abundance of *Desmodus rotundus*. The dominance of *C. perspicillata* (31% of captures) in the coastal forest is an equivocal indicator.

Watt (1998), on the other hand, provided a critique of indirect measures to assess whether a forest is disturbed or not and suggested that research should focus on the type and severity of habitat disturbance rather than species-abundance models. He argued that direct ways of assessing forest disturbance such as visual evidence and local records of logging history are simpler, faster, more reliable, and free of assumptions about the impact of disturbance. Additionally, species-abundance models provide no quantitative measure of the degree of forest disturbance. By these criteria, we would consider the reserve a regenerating, non-fragmented landscape with pockets of old-growth forest.

Netting Effort.—We captured approximately twice as many bats per meter-hour of net inland (0.174 bats per m-hour of net) as we did along the coast (0.085 bats per m-hour of net). Most of these netting sessions were during the rainy season. We found that we caught so few bats along the coast during the dry season that we could not fashion a tenable field problem to keep students occupied. Our impressions that there were many fewer bats in the coastal forest during the dry season than during the rainy season therefore remain subjective. Dry season captures inland were extremely high when our nets were placed over isolated pools in the Quebrada San Miguel streambed. In the late dry season (April 2004), for example, we captured more than 50 bats in a 45-min period in 2 nets set over 1 large pool and a nearby small pool.

If we multiply our capture rates by 12 to evaluate capture rates in terms of captures per hour per 12 m net, we can compare our net success with values obtained by other workers. We caught approximately 1.02 bats per 12 m net-hour along the coast and 2.09 bats per 12 m net-hour in the inland forest. Elsewhere in Costa Rica, LaVal (2004a, 2004b) reported capture rates for wet forest at La Selva (1.05 bats per net-hour), 2 cloud forest habitats at Monteverde (0.94 in primary cloud forest, 1.65 in secondary cloud forest), and in dry forest at Santa Rosa (1.41 bats per 12 m net; from Fleming, 1988). Fenton et al. (1992) captured 0.2 to 2.2 bats per 12 m net per hour in various undisturbed forest habitats in Akumal, Mexico. Our capture rates in the inland forest are among the highest of all these rates. However, these comparisons should be taken only as approximations because a 12–m net will rarely, if ever, capture twice as many bats as a 6-m net, particularly if nets are set across narrow flyways.

Anabat Acoustical Survey.—In late February 2005 Richard K. LaVal conducted a 4-night acoustical survey near the Estación Biológica San Miguel using the Anabat bat-detecting system to detect and identify ultrasonic signals from free-flying bats. Based on their echolocation signatures, he identified the following 16 species of bats: *Balantiopteryx plicata*, *Diclidurus albus*, *Peropteryx macrotis*, *Saccopteryx bilineata*, *Saccopteryx leptura*, *Noctilio leporinus*, *Lasiurus blossevillii*, *Lasiurus ega*, *Myotis elegans*, *Myotis nigricans*, *Myotis riparius*, *Rhogeessa tumida*, *Eumops* (cf *underwoodi* or *auripendulus*), *Molossus*

ater, *Molossus molossus*, and *Nyctinomops laticaudatus* (LaVal, pers. comm.). Of these, 8 species—*Peropteryx macrotis*, *Saccopteryx leptura*, *Lasiurus blossevillii*, *Myotis elegans*, *Eumops* sp., *Molossus ater*, *M. molossus*, and *Nyctinomops laticaudatus*—were not taken in mist nets by us on any other occasion. The most commonly recorded bat was *Saccopteryx leptura* followed by *S. bilineata*. This is the southernmost record for *Myotis elegans*.

Microhabitat Associations of Bats.—Habitat segregation exists even over the relatively short distance (less than 1 km) between our coastal and inland forest sites. *Glossophaga soricina* and *Uroderma bilobatum* were netted along the coast, whereas *Trachops cirrhosus* was netted only inland. Six species—*Artibeus jamaicensis*, *A. watsoni*, *Carollia perspicillata*, *Desmodus rotundus*, *Sturnira lilium*, and *Rhogeessa tumida*—were netted equally in both areas. We stress that our sampling efforts were not distributed over the year, but rather were focused almost exclusively in July and February, with 1 session in April. If the different species of bats are tracking food sources that are different or out of synchrony in the coastal and interior forests, we would be unable to resolve the issue of microhabitat associations until we have a better understanding of seasonal abundances of the various bat species.

We expect that additional netting will expand the number of species found in both habitats, especially for species represented by low numbers. For example, *Artibeus lituratus* and *Choeroniscus godmani* (known from the coast in small numbers) may well turn up in the forest and *Lasiurus ega* (known only from inland) also may use coastal habitat. The concentration of *Trachops cirrhosus* in the forest may be a true habitat choice, possibly based on the abundance of prey items (large insects and frogs) inland. *Uroderma bilobatum* roost in the young *Attalea* palms along the coast, and perhaps they restrict their foraging to this neighborhood during the July and February seasons of our netting efforts.

Seasonal Abundances of Bats.—We found some evidence of differences in seasonal abundance of species at Cabo Blanco. *Balantiopteryx plicata*, *Saccopteryx bilineata*, *Noctilio leporinus*, *Artibeus watsoni*, *Desmodus rotundus*, *Glossophaga soricina*, *Phyllostomus hastatus*, *Trachops cirrhosus*, *Lasiurus ega*, and *Myotis nigricans* seem to be equally abundant in both seasons. In contrast, *Artibeus jamaicensis*, *Carollia perspicillata*, *Sturnira lilium*, *Uroderma bilobatum*, and *Rhogeessa tumida* were abundant (or at least present) in the rainy season but uncommon during the dry season. No species was more abundant in the dry season than the rainy season.

Bats that utilize the caves (*Balantiopteryx plicata*, *Saccopteryx bilineata*, *Desmodus rotundus*, and *Phyllostomus hastatus*) were present in comparable population sizes during rainy and dry seasons. *Uroderma bilobatum* abandoned its roosting sites in the coastal *Attalea* palms during the dry season and we never saw more than 1 or 2 individuals during the dry seasons.

Do individuals of 1 or more species move out of the region during certain seasons? Seasonal migrations have long been known for north-temperate bats, as well as for birds and butterflies. Recently however, seasonal altitudinal migrations have been shown for Costa Rican birds (Stiles and Skutch, 1989), butterflies (Haber and Stevenson, 2004), and bats (Timm and LaVal, 2000; Stoner, 2001; LaVal, 2004a, Stoner and Timm, 2004). In recent years, it has become apparent that bats in Costa Rica (and presumably elsewhere in Central America) move considerable distances, probably

in response to seasonal variation in food resources and, at times, probably because of inclement weather. Timm and LaVal (2000) documented that several species of middle- and high-elevation species show strong seasonal variation in abundance that they interpreted as migrations into and out of the area. They suggested that these bats were tracking seasonal increases and decreases in abundance of preferred foods (also see LaVal, 2004a, 2004b). With additional capture data we hope to evaluate the relative abundance of males and female in both the rainy season and dry season.

Food Availability for Bats.—A number of species in the pantropical family Moraceae are found at Cabo Blanco; the best known members are the figs. The diversity and abundance of figs found here provide an especially rich food source for bats and other mammals. At least 6 species of figs in the genus *Ficus* occur in the Reserve. Other species of free-standing trees in the Moraceae that produce fruits eaten by bats at Cabo Blanco include *Brosimum alicastrum*, *B. costaricanum*, *Clarisia biflora*, *Pseudolmedia spuria*, and *Trophis racemosa*. *Brosimum alicastrum* and *Trophis racemosa* are the 2 most abundant species of Moraceae found throughout the reserve. *Brosimum alicastrum* and *B. costaricanum* can produce massive fruit crops (Camacho-Céspedes and Lindquist in press). *Artibeus jamaicensis*, a fig specialist, was one of the most abundant bats at Cabo Blanco. We captured it both during the rainy and dry seasons, but it was more abundant in the rainy season. Interestingly, *Artibeus lituratus*, another fig specialist, was an uncommon bat at Cabo Blanco.

Species of the understory shrub *Piper* comprise an essential food source for bats of the genera *Carollia* and *Sturnira*. At Cabo Blanco, *Piper* grows abundantly away from the maritime influence and is most abundant along streams. Two species of *Piper*, *P. reticulatum* and *P. tuberculatum*, are known from the reserve, with *P. reticulatum* common and producing flowers and fruit throughout the year (Camacho-Céspedes and Lindquist in press). With the exception of *Glossophaga soricina*, the nectar-feeding bats of the subfamily Glossophaginae are not well represented at Cabo Blanco either in terms of species diversity or abundance. *Pachira quinata*, a common canopy tree throughout the reserve, is fed upon and flowers pollinated by nectar bats, presumably *G. soricina*, but this remains unstudied. The seasonal variation in abundance of food and water likely are critical to a number of bat species, but the details remain untested at Cabo Blanco. At Cabo Blanco, the nectar feeding bat community is not as diverse as at other sites in Costa Rica such as La Selva, Monteverde, and Palo Verde.

Comparison with Palo Verde, a Dry Forest Site.—In comparing the species diversity and abundances of bats at Cabo Blanco to those seen at Costa Rica's Parque Nacional Palo Verde, we find both similarities and differences. Palo Verde is located in tropical dry forest of the Guanacaste lowlands ca. 84 km north of Cabo Blanco, and is considerably drier than Cabo Blanco; Timm has been working there since 1974 (see Stoner and Timm, 2004; Timm, unpubl.). Both sites have species that either are not present at the other site or are found there in quite different abundances. Interestingly, both the similarities and differences in the bat faunas between the sites represent most of the major feeding niches. Species that are found in similar relative abundances at both sites include *Balantiopteryx plicata*, *Saccopteryx bilineata*, *Artibeus jamaicensis*, *Artibeus watsoni*, *Carollia perspicillata*, *Chrotopterus auritus*, *Desmodus rotundus*, *Sturnira lilium*, *Trachops cirrhosus*, *Uroderma bilobatum*, *Vampyrum spectrum*, and *Rhogeessa tumida*. One species, *Phyllostomus hastatus*, is common at Cabo Blanco, but not yet recorded at Palo

Verde despite extensive netting and cave surveys there over several years. The other large predaceous bats (*C. auritus*, *T. cirrhosus*, and *V. spectrum*) are seen in similar abundances at the two sites. *Glyphonycteris sylvestris* and *Lophostoma silvicolum*, which are rare at Cabo Blanco, have yet to be recorded at Palo Verde. In contrast, Palo Verde has a richer fauna of the small and mid-sized phyllostomines than is seen at Cabo Blanco.

Species that are found in moderate abundance at Palo Verde, but not yet recorded from Cabo Blanco, include *Pteronotus davyi*, *P. gymnonotus*, *Carollia subrufa*, *Centurio senex*, *Micronycteris minuta*, and *Natalus stramineus*. Species that are relatively common at Palo Verde but rare at Cabo Blanco include *Pteronotus parnellii* and *Artibeus lituratus*. Species that are rare at both sites include *Diclidurus albus*, *Carollia castanea*, and *Myotis riparius*.

Artibeus jamaicensis is an abundant species at Cabo Blanco, comprising 25% of our captures, and also is abundant at Palo Verde, where it constitutes 13.9% of captures (Stoner and Timm, 2004). Similarly, *Carollia perspicillata* comprises 27% of our captures at Cabo Blanco and roughly 10% of our captures at Palo Verde. Stoner and Timm (2004) found *S. lilium* to be one of the most abundant species of bats at Palo Verde; however, we observed this species at Cabo Blanco only during the rainy season, and it clearly was not as abundant there as it is at Palo Verde. *Pteronotus parnellii* was fairly common at Palo Verde and captured there regularly both in the rainy and dry seasons; in contrast, we caught a single adult female at Cabo Blanco in the dry season. Additionally, nets set over water at Cabo Blanco late in the dry season catch large numbers of bats very quickly, which also is our experience at Palo Verde.

In the caves of Refugio de Vida Silvestre Cueva Los Murciélagos, we regularly observed *Balantiopteryx plicata*, *Saccopteryx bilineata*, *Desmodus rotundus*, and *Phyllostomus hastatus* during both the rainy and dry seasons. In the Cueva del Tigre complex at Palo Verde, we also observed *B. plicata*, *S. bilineata*, and *D. rotundus*, roosting both in the rainy and dry seasons; however, we have never observed *P. hastatus* there. The large phyllostomine roosting in the caves there was *Chrotopterus auritus*, which was found year-round; it has not been seen roosting in any of the caves at Refugio de Vida Silvestre Cueva Los Murciélagos.

In tropical dry forest and moist forest, ground level nets are very effective at sampling bat diversity, especially when nets are placed over water in the dry season. Canopy level netting, which has proven successful elsewhere in the tropics, may not be as effective in these forests in detecting additional species because of the low canopy height. There is no doubt that additional survey techniques such as acoustical surveys with electronic bat detectors to detect and identify ultrasonic signals from bats will increase the number of species known from Cabo Blanco. Additional netting will increase the species list, but we do not predict that this increased effort will make the species inventory congruent with that of Palo Verde.

Conservation.—Bats were extremely abundant at Cabo Blanco, especially species of nectarivorous and frugivorous phyllostomids. Critical to regeneration of tropical forests is the ability of seeds to move from the parent plant to new areas. LaVal (2004a) reported that bats disperse more seeds than do birds, that pioneer species of plants are especially well represented in bat-dispersed seeds, and that these seeds are dispersed primarily to disturbed areas. Bats, because of their high mobility, can disperse large numbers of seeds for considerable distances. Bats at Cabo Blanco face large fluctuations

in the availability of food resources during the year, and may well be tracking the abundance of preferred foods.

In summary, the bat fauna in and around 40-year-old regenerating forest of Costa Rica's Reserva Natural Absoluta Cabo Blanco is diverse and many species, especially those that are the primary dispersers of seeds, are extremely abundant. The largest carnivores are present, but the small and middle-sized predators are poorly represented. Several species have clear habitat preferences and seasonal differences occur in abundance and reproductive patterns. Finally, the species composition and abundances differ somewhat from the relatively close, dry forest site, Palo Verde. Because of their high mobility, perhaps bats, more than most other mammals, follow the prophecy (slightly corrupted) from the 1989 movie *Field of Dreams*: if you preserve it … they will come.

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