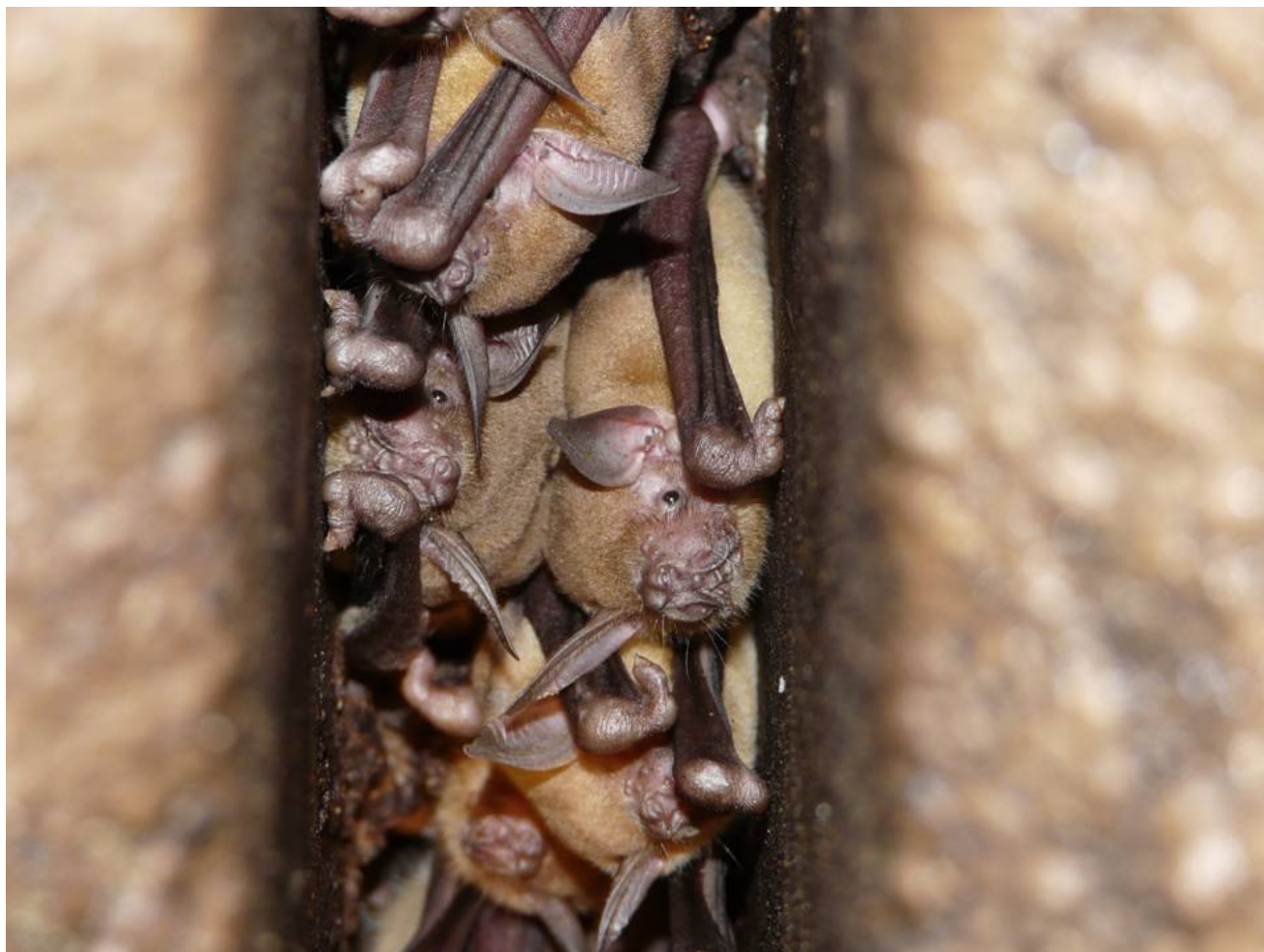




# LESSER BULLDOG BAT

*Noctilio albiventris* Desmarest, 1818



**FIGURE 1** - (FPMAM104PH) Roosting adults, Pozo Colorado, Departamento Presidente Hayes (Paul Smith October 2009).

**TAXONOMY:** Class Mammalia; Subclass Theria; Infraclass Metatheria; Order Chiroptera; Suborder Microchiroptera; Superfamily Noctilionoidea; Family Noctilionidae (Hofer et al 2003, López-Gonzalez 2005, Myers et al 2006). The genus *Noctilio*, Linnaeus 1766, is the only genus in the family and contains two species, both of which are present in Paraguay. The origin of the generic name *Noctilio* is derived from the Latin “noctis” meaning “night” or perhaps from the French Noctilion meaning “bat” from the same root (Palmer 1904). The species name *albiventris* is Greek meaning “white-bellied” (Braun & Mares 1995).

This species was for a long time referred to by the name *Noctilio labialis* until it was demonstrated that that name referred to a specimen of *N. leporinus* (Hershkovitz 1975, Davis 1976) and prior to that was placed in the genus *Dirias* (Thomas 1920). The name *Noctilio ruber* (Rengger 1830) based on Azara’s “chauve-souris onzieme,” from Paraguay was believed to refer to this species by Hershkovitz (1975) but according to Davis (1976) the name clearly refers to a *Myotis*, and probably *Myotis ruber*. No type specimen apparently exists and Cabrera (1958) fixed the type locality as Rio São Francisco, Bahía, Brazil as the first

published locality for the species by Spix (1823). *Noctilio albiventer* Desmarest (1820) is based on the "Noctilion à ventre blanc" of E. Geoffroy St.Hilaire and Pennant's (1971) Peruvian Bat Var. β". It is not possible to determine whether this name change from Desmarest's own work (1818) is due to an unjustified emendation of the original name or simply a spelling error.

There are four recognised subspecies, that present in Paraguay is *N.c.cabrerae* Davis 1976 (Type Locality Fuerte Olimpo, Departamento Alto Paraguay, Paraguay). Supposedly this subspecies is distinguished by paler colouration and smaller size when compared to other populations, but there is convincing circumstantial evidence to suggest that size change across the species range is clinal with populations at the northern and southern extremes of the range averaging larger and there is considerable variation in colour between individuals at any one given site. Myers & Wetzel (1983) considered that the size differences did not warrant subspecific separation, but this was refuted by Taddei et al (1986) who found considerable differences in size between a population in southeastern Brazil and those in Paraguay which they believed sufficient to confirm their subspecific separation. However Myers & Wetzel (1983) had previously noted that specimens from central and southern Paraguay were similar in size to those of Beni Province, Bolivia, but much smaller than those that occurred in the intervening area of Santa Cruz, Bolivia.

Gardner synonymised *N.a.affinis* WB Davis 1976, with *N.a.albiventris*. López-González (2005) stated that a revision of the geographic variation of the species was necessary before conclusions could be drawn and elected not to assign the Paraguayan populations to subspecies pending such a study. Synonyms adapted from Hood & Pitocchelli (1983), López-Gonzalez (2005) and Gardner (2007):

*Noctilio albiventris* Desmarest 1818:15. Type locality "L'Amérique Meridionale". Restricted to Rio São Francisco, Bahía, Brazil by Cabrera (1958) on the basis of Spix (1823).

*Noctilio albiventer* Desmarest 1820:118. Unjustified emendation or incorrect spelling.

*Noctilio albiventer* Spix 1823:58. Type locality "Fluviem St Francis" (=Rio São Francisco, Bahía, Brazil).

*Noctilio affinis* d'Orbigny 1837: Plate 10, fig 1. Type locality "Concepción", Beni, Bolivia, based on d'Orbigny & Gervais (1847).

*Dirias albiventer* Miller 1906:84. Name combination.

*Noctilio zaparo* Cabrera 1907:57. Type locality "Ahuano on Rio Nap" Napo, Ecuador.

*Noctilio minor* Osgood 1910:30. Type locality "Encontrados, Zulia, Venezuela".

*Noctilio albiventer minor* Osgood 1912:62. Name combination.

*Dirias zaparo* JA Allen 1916:225. Name combination.

*Dirias irex* O. Thomas 1920:273. Type locality "Santa Julia, Rio Iriri, Rio Xingú" Pará, Brazil.

*Dirias albiventer minor* Goldman 1920:117. Name combination.

*Dirias albiventer albiventer* Cabrera 1930:426. Name combination.

*Dirias minor* Goodwin 1942:211. Name combination.

*Noctilio (Dirias) albiventer* Sanborn 1949:279. Name combination.

*Noctilio labialis* Hershkovitz 1949:434. Not *Noctilio labialis* Kerr (1792).

*Noctilio labialis albiventer* Hershkovitz 1949:434. Name combination.

*Noctilio labialis labialis* Hershkovitz 1949:434. Name combination.

*Noctilio labialis minor* Hershkovitz 1949:433. Name combination.

*Noctilio labialis albiventris* Cabrera 1958:55. Name combination.

*Noctilio labialis zaparo* Cabrera 1958:56. Name combination.

*Noctilio albiventris albiventris* Hershkovitz 1975:244. First use of current subspecific name.

*Noctilio albiventris minor* Hershkovitz 1975:244. First use of current subspecific name.

*Noctilio albiventris ruber* Hershkovitz 1975:244. Name combination. Not *Vespertilio ruber* Rengger (1830).

*Noctilio albiventris zaparo* Hershkovitz 1975:244. Name combination.

*Noctilio albiventris affinis* WB Davis 1976:687. First use of current subspecific name.

*Noctilio albiventris cabrerai* WB Davis 1976:701. Type locality "Fuerte Olimpo, Depto. de Olimpo (=Alto Paraguay), Paraguay".

**ENGLISH COMMON NAMES:** Lesser Bulldog Bat (Hood & Pitocchelli 1983, Barquez, Giannini & Mares 1993, Eisenberg 1989, Wilson & Cole 2000), Southern Bulldog Bat (Redford & Eisenberg 1992), Little Bulldog Bat (Rasweiler 1977), Lesser Noctilio (Davis 1976).

**SPANISH COMMON NAMES:** Murciélago pescador chico (Barquez, Giannini & Mares 1993), Murciélago bulldog menor (Emmons 1999), Pescador menor (Redford & Eisenberg 1992), Pescador chico (Massoia et al 2006), Noctilio menor vientre blanco (Massoia et al 2006)..

**GUARANÍ COMMON NAMES:** Mbopi pyta (Emmons 1999).

**DESCRIPTION:** This is a large bat, with a protruding nose lacking a nose leaf, and a strongly swollen and cleft forelip which exposes the large canines and pointed incisors. The chin is prominent and has conspicuous lateral ridges, and there are internal cheek pouches. The forward-leaning ears are separate, long, narrow and pointed with a lobed tragus. Ears are naked and brownish and furred only at the base. The tail is more than half the femoral length and extends to about half the uropatagial length, the tip of the tail pointing free on the dorsal surface. Uropatagium extends beyond the large and robust feet (though less so than in *N.leporinus*) and there is a well-developed bony calcaneus. Pelage short. Paraguayan specimens are typically brownish dorsally, with a small proportion of the population more rufous-orange in colour. Typically there is little difference in colour between the dorsum and the venter. A thin longitudinal line along the dorsal surface, from the interscapular region to the rump, is usually paler than the rest of the pelage, but is barely discernible in some specimens. Barquez et al (1999) note that sexual dimorphism in colour is common with females typically browner than males. Wings long, narrow and pointed. Wing and tail membranes are brown and semitranslucent. Flanks naked. Live specimens have a strong musky odour.

**CRANIAL CHARACTERISTICS:** Characteristics as for family (Miller 1907). Males are larger in all measurements than females and adults have a more developed sagittal crest. Taddei et al (1986) found mastoid width and width across upper canines to be the most reliable determinants of sex in skulls of this species.

The following measurements are based on a series of Paraguayan specimens published in López-González (2005) for northern (1), central (2) and southern (3) localities respectively in Paraguay: **1** Estancia Doña Julia, Departamento Alto Paraguay 20°10.98'S, 58°09.42'W: *Greatest Skull Length* male 19.9mm (+/- 0.6mm) female 19.7mm (+/- 0.13mm); *Condylbasal Length* male 18.8mm (+/- 0.3mm) female 18.5mm (+/- 0.66mm); *Transverse Zygomatic Width* male 15.6mm (+/- 0.27mm) female 15.4mm (+/- 0.02mm); *Mastoid Width* male 15.6mm (+/- 1.03mm) female 14.6mm (+/- 1.14mm); *Interorbital Constriction* male 5.9mm (+/- 0.2mm) female 5.8mm (+/- 0.27mm); *Width Across Upper Molars* male 9.8mm (+/- 0.24mm) female 9.8mm (+/- 0.24mm); *Width Across Upper Canines* male 7mm (+/- 0.21mm) female 6.6mm (+/- 0.34mm). **2** 17km east of Luque, Departamento Central: *Greatest Skull Length* male 20.7mm (+/- 0.77mm) female 19.4mm (+/- 0.45mm); *Condylbasal Length* male 19.6mm (+/- 0.38mm) female 18.6mm (+/- 0.52mm); *Transverse Zygomatic Width* male 15.7mm (+/- 1.43mm) female 15.1mm (+/- 0.33mm); *Mastoid Width* male 15.7mm (+/- 1.43mm) female 14.3mm (+/- 0.36mm); *Interorbital Constriction* male 6.1mm (+/- 0.1mm) female 5.8mm (+/- 0.19mm); *Width Across Upper Molars* male 10.1mm (+/- 0.29mm) female 9.6mm (+/- 0.26mm); *Width Across Upper Canines* male 7.3mm (+/- 0.35mm) female 6.6mm (+/- 0.22mm). **3** Departamento Misiones: *Greatest Skull Length* male 21.4mm (+/- 0.86mm) female 19.7mm (+/- 0.41mm); *Condylbasal Length* male 20.2mm (+/- 0.38mm) female 19.1mm (+/- 0.28mm); *Transverse Zygomatic Width* male 16.5mm (+/- 0.32mm) female 15.4mm (+/- 0.45mm); *Mastoid Width* male 16.6mm (+/- 1.33mm) female 14.8mm (+/- 0.3mm); *Interorbital Constriction* male 6.2mm (+/- 0.23mm) female 6.1mm (+/- 0.12mm); *Width Across Upper Molars* male 10.2mm (+/- 0.16mm) female 9.9mm (+/- 0.24mm); *Width Across Upper Canines* male 7.4mm (+/- 0.23mm) female 6.7mm (+/- 0.17mm).

Barquez et al (1999) give the following measurements for individuals from Argentina (n=5 unless stated): *Greatest Skull Length* 21.1mm (+/- 0.44mm); *Condylbasal Length* 19mm (+/- 0.68mm, n=4); *Zygomatic Width* 15.6mm (+/- 0.66mm); *Mastoid Width* 13.8mm (+/- 0.87mm); *Interorbital Constriction* 6mm (+/- 0.16mm); *Postorbital Constriction* 8.6mm (n=1); *Width Across Upper Molars* 9.9mm (+/- 0.13mm); *Width Across Upper Canines* 7.3mm (+/- 0.23mm); *Palatal Length* 9.3mm (+/- 0.24mm); *Length of Mandible* 14.9mm (+/- 0.21mm); *Width of Braincase* 11.4mm (+/- 0.56mm).

Taddei et al (1986) gave the following measurements for a sexed sample (n=20 males, n=30 females) from São Paulo State, Brazil: *Greatest Skull Length* male 21.76mm (+/- 0.58mm) female 20.07mm (+/- 0.31mm); *Condylbasal Length* male 19.05mm (+/- 0.35mm) female 18.01mm (+/- 0.25mm); *Transverse Zygomatic Width* male 15.20mm (+/- 0.42mm) female 14.21mm (+/- 0.27mm); *Mastoid Width* male 14.72mm (+/- 0.80mm) female 13.21mm (+/- 0.47mm); *Interorbital Constriction* male 6.05mm (+/-



0.14mm) female 5.89mm (+/- 0.16mm); *Width Across Upper Molars* male 9.47mm (+/- 0.17mm) female 9.03mm (+/- 0.17mm); *Width Across Upper Canines* male 7.08mm (+/- 0.20mm) female 6.32mm (+/- 0.14mm); *Condylacanine Length* male 18.02mm (+/- 0.32mm) female 16.95mm (+/- 0.22mm); *Base Length of Skull* male 16.56mm (+/- 0.28mm) female 15.75mm (+/- 0.23mm); *Length of Mandible* male 13.88mm (+/- 0.36mm) female 12.87mm (+/- 0.18mm); male 19.05mm (+/- 0.35mm) female 18.01mm (+/- 0.25mm); *Width of Braincase* male 11.37mm (+/- 0.24mm) female 11.12mm (+/- 0.21mm).

**DENTAL CHARACTERISTICS:** I2/1 C1/1 P 1/2 M 3/3 = 28. As for family. Upper M1 and M2 are almost equal without posterior emargination and lacking any clear gap between them. Hypocone relatively larger than in *N.leporinus* and connected by a high, conspicuous commissure extending from the protocone to the metacone. (Miller 1907).

The following measurements are based on a series of Paraguayan specimens published in López-González (2005) for northern (1), central (2) and southern (1) localities respectively in Paraguay: **1** Estancia Doña Julia, Departamento Alto Paraguay 20°10.98'S, 58°09,42'W: *Upper Tooth Row* male 7.6mm (+/- 0.21mm) female 7.4mm (+/- 0.26mm); *Lower Tooth Row* male 8.2mm (+/- 0.22mm) female 7.9mm (+/- 0.32mm). **2** 17km east of Luque, Departamento Central: *Upper Tooth Row* male 7.3mm (+/- 0.35mm) female 7.6mm (+/- 0.23mm); *Lower Tooth Row* male 8.6mm (+/- 0.25mm) female 8.1mm (+/- 0.2mm). **3** Departamento Misiones: *Upper Tooth Row* male 8mm (+/- 0.1mm) female 7.6mm (+/- 0.2mm); *Lower Tooth Row* male 8.7mm (+/- 0.17mm) female 8.2mm (+/- 0.16mm).

Barquez et al (1999) give the following measurements for individuals from Argentina (n=5): *Upper Tooth Row* 8.1mm (+/- 0.45mm); *Lower Tooth Row* 7.4mm (+/- 0.19mm).

Taddei et al (1986) gave the following measurements for a sexed sample (n=20 males, n=30 females) from São Paulo State, Brazil: *Upper Tooth Row* male 7.76mm (+/- 0.15mm) female 7.18mm (+/- 0.11mm); *Lower Tooth Row* male 8.22mm (+/- 0.15mm) female 7.75mm (+/- 0.11mm).

**GENETIC CHARACTERISTICS:** 2n=34 FN=62. (Eisenberg & Redford 1999). As for family (Baker & Jordan 1970).

**EXTERNAL MEASUREMENTS:** A large bat though the smaller member of its family. There is marked sexual dimorphism in size with males larger than females.

The following measurements are based on a series of Paraguayan specimens published in López-González (2005) for northern (1), central (2) and southern (1) localities respectively in Paraguay: **1** Estancia Doña Julia, Departamento Alto Paraguay 20°10.98'S, 58°09,42'W **TL** male 99.2 (+/- 4.80mm), female 93.7mm (+/- 4.62mm); **TA** male 20.2mm (+/- 3.80mm), female 17.1mm (+/- 0.73mm); **FT** male 17.2mm (+/- 1.3mm), female 16.3mm (+/- 0.58mm); **FA** male 60.6mm (+/- 1.86mm), female 59.3mm (+/- 0mm); **EA** male 23.8mm (+/- 0.99mm), female 23.7mm (+/- 2.08mm); *Length of Third Digit* male 54.6mm (+/- 0.86mm), female 53.4mm (+/- 0mm) **WT** male 30.7g (+/- 4.22mm), female 26.2g (+/- 3.09mm). **2** 17km east of Luque, Departamento Central **TL** male 99.2mm (+/- 2.39mm), female 92.8mm (+/- 4.09mm); **TA** male 18.2mm (+/- 0.45mm), female 17.4mm (+/- 1.14mm); **FT** male 17.4mm (+/- 1.14mm), female 16.8mm (+/- 0.84mm); **FA** male 63.9mm (+/- 1.44mm), female 62.1mm (+/- 1.2mm); **EA** male 26.6mm (+/- 1.14mm), female 24.8mm (+/- 1.1mm); *Length of Third Digit* male 56.4mm (+/- 1.51mm), female 55.4mm (+/- 1.36mm) **WT** male 36g (+/- 4.3mm), female 31.6g (+/- 2.19mm). **3** Departamento Misiones **TL** male 97.9mm (+/- 6.39mm), female 104.1mm (+/- 6.01mm); **TA** male 20.3mm (+/- 4.40mm), female 20.3mm (+/- 2.12mm); **FT** male 18.5mm (+/- 2mm), female 17.5mm (+/- 1.2mm); **FA** male 66mm (+/- 0mm), female 63.6mm (+/- 0mm); **EA** male 22.3mm (+/- 1.49mm), female 22.1mm (+/- 1.07mm); *Length of Third Digit* male 60.7mm (+/- 0mm), female 58.1mm (+/- 0mm); **WT** male 43.2g (+/- 5.73mm), female 33.5g (+/- 2.82mm).

Barquez et al (1999) give the following measurements for individuals from Argentina (n=5 unless stated): **TL** 95mm (+/- 2.72mm, n=4); **TA** 11.4mm (+/- 0.49mm, n=4); **FT** 14.5mm (+/- 0.53mm, n=4); **FA** 63.3mm (+/- 2.46mm, n=12); **EA** 19.9mm (+/- 1.42mm, n=4).

Taddei et al (1986) gave the following measurements for a sexed sample (n=20 males, n=30 females) from São Paulo State, Brazil: **FA** male 61.37mm (+/- 1.53mm), female 59.58mm (+/- 1.33mm); **WT**: male 32.45g (+/- 3.43g, n=16), female 22.40g (+/- 3.11g, n=9); *Length of Third Metacarpal* male 55.35mm (+/- 1.12mm), female 53.09mm (+/- 1.02mm); *Length of First Phalange of Third Digit* male 14.29mm (+/- 0.74mm), female 13.41mm (+/- 0.66mm); *Length of Second Phalange of Third Digit* male 40.28mm (+/- 1.28mm), female 38.70mm (+/- 1.80mm); *Length of Fourth Metacarpal* male 57.09mm (+/-

1.53mm), female 54.36mm (+/- 1.32mm); *Length of First Phalange of Fourth Digit* male 9.49mm (+/- 0.60mm), female 9.09mm (+/- 0.57mm); *Length of Second Phalange of Fourth Digit* male 23.47mm (+/- 1.12mm), female 22.18mm (+/- 1.15mm); *Length of Fifth Metacarpal* male 55.59mm (+/- 1.20mm), female 52.92mm (+/- 1.35mm); *Length of First Phalange of Fifth Digit* male 11.33mm (+/- 0.79mm), female 10.76mm (+/- 0.76mm); *Tibial Length* male 23.36mm (+/- 1.36mm), female 21.91mm (+/- 1.17mm).

**SIMILAR SPECIES:** Bulldog bats can be immediately recognised on account of their large size, pointed ears, massive feet and "hare-lip". The two component species however are extremely similar to each other and can be distinguished with certainty only on the basis of size and body measurements. This is the smaller of the two species with forearm length <70mm, hindfoot length <27mm, and the combined length of the tibia and hindfoot is less than 70% of the forearm length. The confusion species *Noctilio leporinus* has a forearm length >80mm, hindfoot length >28mm and the combined length of the tibia and hindfoot is greater than 80% of the forearm length. Hood & Pitocchelli (1983) further state that this species generally has a wingspan c400mm and weight c40g compared to c500mm and c50g in *leporinus*.

When comparing skulls the condylobasal length is <21mm in this species and >21mm in *leporinus*. Though there may be some overlap between the largest *albiventris* and smallest *leporinus* in other skull measurements, Hood & Pitocchelli (1983) note that the length of the maxillary tooththrow is rarely more than 8mm in *albiventris* and rarely less than 9mm in *leporinus*. Upper M1 and M2 of *leporinus* are clearly separated unlike those of this species.

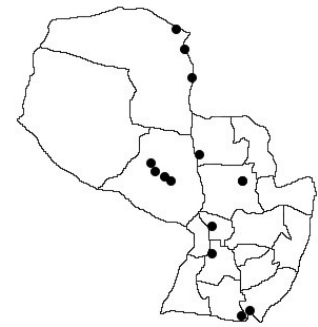
**DISTRIBUTION:** The species has a wide but discontinuous range from Guatemala and Honduras to northern Argentina and western Uruguay. Its range along the Pacific coast of Central America is patchy and it is absent from large areas of South America, including the Cerrado belt of Brazil and much of Colombia, Ecuador and Peru west of the Andes. Davis (1976) attributed the populations to four subspecies: *N.a.minor* Osgood 1910, occurring in Central America and northern Colombia and Venezuela; *N.a.albiventris* Desmarest 1818, along the eastern Amazon watershed and coast of Brazil, extending north into southeastern Venezuela and southwestern Guyana; *N.a.affinis* WB Davis 1976, with an unusual range in central and northern Bolivia, eastern Peru, Ecuador and Colombia, the western Amazon of Brazil, a thin finger through central Venezuela to the Caribbean coast where it extends east coastally through the Guianas to extreme northern Brazil; *N.a.cabreraei* WB Davis 1976, Paraguay, southern Bolivia, southern Brazil, northern Argentina and western Uruguay; however see the taxonomic section for a discussion of the validity of these subspecies.

In Bolivia the species has been recorded from Departamentos Pando, Beni, Cochabamba and Santa Cruz (Aguirre 2007). In Brazil the species is widely distributed, having been recorded in the following states: Acre, Amazonas, Amapá, Bahía, Minas Gerais, Mato Grosso, Mato Grosso do Sul, Pará, Piauí, Paraná, Roraima and São Paulo (dos Reis et al 2007).

In Argentina it has been recorded in Provincias Corrientes, Misiones, Santa Fé, Chaco and Formosa (Barquez et al 1999). Cabrera (1938) considered Burmeister's (1879) record of *N.leporinus* in Provincia Salta to refer to this species based on the given description, but according to Barquez et al (1999) this species has never been recorded in northwestern Argentina.

In Paraguay this species seems to be distributed along the Rios Paraguay and Paraná and their tributaries, at least as far east as Departamento Itapúa, and inland in seasonally-flooded areas of Departamento Presidente Hayes in the Humid Chaco. *Noctilio* bats seen foraging along the Rio Paraná in Encarnación presumably belong to this species, representing an eastward expansion from the published Paraguayan range - though the specific identity of these individuals remains to be confirmed (P.Smith pers.obs.). The only confirmed record of this species in Provincia Misiones is from Posadas, on the opposite bank of the Rio Paraná from Encarnación (Massoia et al 2006).

**HABITAT:** Associated with larger freshwater bodies, stagnant or with a slow current, including along the Rios Paraguay and Paraná and its major tributaries. In the Humid Chaco it exploits areas of suitable habitat created by periods of seasonal flooding, expanding into the palm savanna, but disappears from the same



regions in times of drought. It seems that presence of suitable water courses is the limiting factor on its distribution and it even occurs in areas of human habitation where such conditions are met. However Myers & Wetzel (1983) note that distribution is patchy in the Chaco region and semi-isolated populations may be composed of very few individuals. Bernard & Fenton (2003) noted that the species may roost a considerable distance from suitable foraging areas and crosses unsuitable habitat with a fast, direct flight 5 to 6m from the ground and not attempting to pursue insects encountered en route.

**ALIMENTATION:** Insectivorous. Fleming et al (1972) noted that in Panama 55% of 51 captured individuals had food in their stomachs with combined results consisting of 100% insect material.

**Foraging Behaviour and Diet** Typically foraging occurs over standing or slow-moving water, often in large groups. Kalko et al (1998) described individuals in Costa Rica and Panama as either foraging close to the shore of rivers and tracing a figure-of-eight flight pattern, or foraging 20-30m from the shore in large, meandering circles.

Insects may be taken aerially or from the water surface using the enlarged hind feet to grasp the insect. Echolocation is used when taking insects from the water (Nowak 1991). Individuals which approach the water mouth first are apparently drinking and not hunting. Bats fitted with radiotransmitters in Costa Rica showed little consistency in their use of foraging areas (Fenton et al 1993).

Kalko et al (1998) documented various search strategies in wild individuals, noting that flexibility in strategies allows them to quickly adjust to prey ability and enhance foraging efficiency. They defined the strategies used as follows (see vocalisations section for echolocation differences associated with these strategies):

1) *High Search Flight* The bat flies at a height of >20cm above the ground or water with continual wing flapping at a rate of c4 wing beats/s and a speed of 7-7.5 m/s. The predominant hunting strategy is to take insects from the air at a height of 2 to 5m above the water. Prey items varied in size from mosquito-sized to moths 1-3cm long. Prey was captured with the uropatagium or additionally occasionally a wing was used to funnel the prey item towards the tail membrane. At the moment of capture flight speed reduces to 1-2m/s. With a downward movement of the head the prey was removed from the uropatagium and presumably stored in the cheek patches. No evidence was found of insects being caught directly with the mouth. Frequently moths were seen to take evasive action, often as a result falling onto the water surface and causing the bat to turn round and pluck the insect from the water using the pointed dip technique. This technique involves the use of the feet, with flight speed reducing to 5-6m/s. The prey was then transferred to the mouth in the same manner. Pointed dips were observed to be successful on 11 of 13 occasions. It was considered that the fluttering movement of the live insect was necessary for the bat to distinguish a potential food item from stationary floating debris.

2) *Low Search Flight* This occurred in about 20% of the observed hunting procedures. The bat flew parallel to and within about 20cm of the water surface. Amplitude of the downstroke was reduced when compared to High Search Flight but the amplitude of the upstroke was the same. Flight speed is reduced from 6.5-7m/s at 4.5m/s at the end of the segment. Such flights were short, usually in the region of 2-5m long before High Search Flight was resumed. Pointed dips were rarely observed as associated with Low Search Flights.

3) *Random Rake* On one occasion thousands of small shrimp (0.5-1cm long) were jumping from the water. The bats approached in Low Search Flight but with the calcars raised so that the uropatagium was folded, and the claws breaking the water surface for distances of 2-5m. Wing beat amplitude was reduced, especially on the downstroke and wing beat rate increased from 5 beats per second in High Search Flight to 6-8 beats per second. Flight speed reduced to 4-5m/s. The rake technique is an energetically costly form of foraging and is used much less often than by the larger *Noctilio leporinus*. It is hypothesised that it is used only when there is a high chance of success, ie when prey is extremely concentrated.

4) *Overland Tactics* Individuals were seen to hawk for insects for 10-15 minutes each night at a height of 15-20cm over a grassy meadow. They were also seen to forage around lights at a height of 3-5m on two occasions at a distance of 300-500m from the river and to fly backwards and forwards between buildings at a similar height.

In a fecal analysis of individuals from Costa Rica and Panama Whitaker & Findley (1980) found only insects with Coleoptera (Dytiscidae and Carabidae), Hemiptera (Lygaeidae), "Homoptera" (Cercopidae), Lepidoptera and Diptera identified. The large water beetle family Dytiscidae predominated



with 22.5% by volume confirming aquatic feeding. Similar results of Coleoptera, Lepidoptera, Hemiptera, Hymenoptera, Diptera, Orthoptera and "Homoptera" were reported for Costa Rica by Hooper & Brown (1968), Nicaragua by Jones et al (1971) and Colombia by Tamsitt & Valdivieso (1963). Hooper & Brown (1968) stated that the identifiable insects in stomach remains ranged from 4 to 20mm in length and all were capable of flight. Schnitzler et al (1994) note that small insects stranded in water and fluttering on the water surface were enough to initiate a capture response from this species but were ignored by the larger *N.leporinus*. Other items recorded in the diet by Howell & Burch (1974) include pollen from *Ceiba* trees (Bombacaceae) as well as an observation record of an individual feeding at a *Brosimum* tree (Moraceae). Dobson (1878) reported seeds of genus *Morus* in the stomachs of several individuals. Barnett et al (2006) found the floor of a small roost of this species in Amazonian Brazil to be littered with elytra of aquatic beetles of the families Hydrophilidae and Gyrinidae and found no fish or lepidopteran remains.

Gonçalves et al (2007) reported results of fecal analysis of 77 samples from three sites in the Pantanal of Brazil with the following results presented as a percentage of total samples: Arthropods - Hemiptera 81%, Coleoptera 64%, Lepidoptera 43%, Diptera 23%, Hymenoptera 9%, Unidentified Arthropods 9%, Araceae 2%; Seeds: *Cecropia pachystachya* 5%, *Ficus guaranitica* 3%, *Maclura tinctoria* 3%, *Ficus pertusa* 2%, *Ficus* sp 2%, *Banara arguta* 2%, Unidentified species A 12%, Unidentified species B 2%, Unidentified species C 2%. Pollen of *Bauhinia unguolata* was found in 4% of samples. Seven of nine plant species recorded in the diet were also utilised by Phyllostomid bats in the same area. The presence of pollen in the samples may have been a by-product of the bat feeding on pollen-feeding insects, but the plant species from which pollen was found is a known bat-pollinated species and two individuals of the species were also captured close to another common pollen source for bats *Hymenaea stigonocarpa*.

Food is chewed twice as in *N.leporinus*, a process that has been likened to "ruminating" (Goodwin 1928). During the first bout of chewing the prey is chewed rapidly and stored in cheek pouches until it has been completely consumed, it is then everted into the mouth for a second bout of chewing prior to swallowing (Bloedel 1955).

**Diet in Captivity** Attempts to make the species capture fish under experimental conditions have largely failed, even in some cases leading to the point of starvation, though captive individuals did eat dead fish that they were presented with (Bloedel 1955) and fish parts and scales were found in stomach contents from Costa Rica by Howell & Burch (1974).

**REPRODUCTIVE BIOLOGY:** Well studied elsewhere but little information available for Paraguay.

**Seasonality** Breeding is seasonal with a single short breeding season annually, probably influenced by the period of greatest insect abundance. In the Chaco Myers & Wetzel (1983) found lactating females in September, pregnant females in August and October and a juvenile in January.

**Bolivia** In Bolivia pregnant females have been recorded from August to November (Anderson 1997). Wilson & Salazar (1989) collected a female pregnant with a 13mm embryo during September in the Estación Biologica Beni.

**Brazil** Barnett et al (2006) document a lactating female in Jaú National Park, Amazonian Brazil on 18 June 2001 (early dry season) and note that males in the Manaus area smelt strongly and had particularly developed scent glands around the same time.

**Colombia** Rasweiler (1977) confirmed highly synchronous breeding in individuals from Colombia with fertilisation and early embryonic development in late February and March.

**Costa Rica** Hooper & Brown (1968) concluded that this species breeds later in the year than *N.leporinus* in Costa Rica.

**Panama** Eight females returning to a roost in Panama on April 9 were pregnant with embryos all at approximately the same stage of development. Only one of four collected on March 4 was pregnant. (Bloedel 1955b).

**Peru** Tuttle (1970) notes two pregnant and one non-pregnant female from Peru on 21 July. Hice et al (2004) found two pregnant, one lactating and two non-reproductive females in northeast Peru during June. Ascorra et al (1991) collected six pregnant females in October in PN Manu.

**Venezuela** A female captured in April 1978 was not pregnant (August & Baker 1982). Females at Hato El Frio, Pure had well-developed fetuses in late January, gave birth from mid-May to early June and lactated until later July. This means that mating likely occurs from late December to January (Ibañez Ulargui 1981).

**Pregnancy** Ova are fertilised in the oviduct where they develop to an advanced state when compared with other Microchiroptera. Litter size is one pup, with a single case of twins in 72 litters reported by Rasweiler (1977).

**Development** Newborns are altricial lacking fur and with eyes closed, they have large feet of similar size to those of adults, and though they are capable of crawling from birth, they grow slowly. The period of parental care of *Noctilio* is longer than any other bat studied except for the Vampire Bat *Desmodus*. Young do not fly until they are 35-44 days old, flying first with the mother and two weeks may pass before they are confident in the air. Brown et al (1983) observed young bats leaving the roost for the first time to lack agility and several were seen to strike concrete posts during their early flights. Young are not weaned until 75-90 days (mean=80.5) but solid food is consumed for the first time at 45 days when they take pre-masticated food from the cheek pouches of the female.

Colour-marking of bats in a captive colony revealed that females attend only their own young which they recognise by virtue of their "isolation call" (see vocalisations section). Under experimental conditions the correct mother retrieved the correct juvenile on 65.6% of occasions - this consisting of allowing the juvenile to attach to the nipple and returning to the cluster. On the other occasions when other individuals responded to the call of another juvenile, there was no retrieval of the young and the bat flew away again apparently recognising its mistake. Distinct differences in the responses of the mothers was noted, with some mothers responding immediately on hearing the isolation call of their offspring, others showing little or no interest and some individuals reacting quickly to all isolation calls irrespective of whether it came from their own offspring or not. By 3 weeks of age the young are less inclined to utter isolation calls and mothers are as a result less responsive and by 4 weeks they actively seek out their mothers amongst the roosting groups of adults. (Brown et al 1983, Eisenberg & Redford 1999).

**GENERAL BEHAVIOUR:** The species has been maintained in captivity and proved to be a good study subject.

**Activity Levels** Typically there appear to be two peaks of activity per night, with an early feeding phase at dusk followed by a second feeding phase shortly after midnight (Eisenberg & Redford 1999) differing from the pattern shown by *N.leporinus*. Hooper & Brown (1968) suggested that this difference in activity period contributes to differences in diet and reproduction and facilitates the sympatry of the two species. Fenton et al (1993) however radiotracked bats in Costa Rica and found that in the majority of cases a single flight was made by any one individual and up to four nightly flights were occasionally performed, with the number undertaken by any one individual varying nightly. Brown et al (1983) observed the majority of the bats leave roosts in Panama at dusk, but that individuals would return to the roost throughout the night. Ascorra et al (1991) recorded peak activity at 7pm in PN Manu, Peru and Barnett et al (2006) also noted a peak of activity in the first 15 minutes after sunset in central Amazonian Brazil. Kalko et al (1998) noted that in Costa Rica and Panama the level of activity varied from night to night but was highest in the first half an hour after sunset and particularly low on bright nights around full moon.

Bernard & Fenton (2003) radiotracked two males and two females in Amazonian Brazil and found the area utilised to be 150-530ha with a maximum linear movement of 10-13km. It was noted that the species was prepared to travel great distances between the roost and foraging sites. Bats all left the roost within a few minutes of each other but dispersed widely to forage and returned within an hour of emergence.

**Roosts** Roosts typically have a strong musky odour characteristic of the species (Nowak 1991).

Myers & Wetzel (1983) report that in the Chaco the species uses hollowed out trunks of Quebracho *Schinopsis* sp trees as roosting places. Two such roosts were found, one with an exit c1m from the ground where the trunk was c30cm thick, the other in a horizontal branch c20cm in diameter and 6m from the ground. In the Bahía Negra area, Departamento Alto Paraguay individuals have been collected roosting in man-made structures from the buildings and installations associated with the Naval Base. At Pozo Colorado, Departamento Presidente Hayes a roost containing 13 individuals was found in building crevices under a road bridge over a marsh in October 2009. The bats shared the roost site with *Eptesicus furinalis* and *Eptesicus diminutus*, though they roosted away from the other species. (Paul Smith pers. obs.). Baud (1989) documented a roost at Rio Ypané, Departamento Concepción which was also occupied by *Desmodus rotundus*, *Macrophyllum macrophyllum* and *Platyrrhinus lineatus*.



In Panama Bloedel (1955b) found roosts of this species in a church and the attic of a house. The species occupied the most inaccessible parts of the attic, and though they maintained monospecific clusters the general roost site was shared with Molossids. Bernard & Fenton (2003) also noted roosting in village buildings in Amazonian Brazil, including occupied houses, in monospecific groups of 50 to 60 individuals. Individuals moved between roosts, occupying the same roost for a minimum of 1 and maximum of ten consecutive nights. Barnett et al (2006) recorded a small colony of five individuals in a deep hole up the centre of a live *Ocotea* (Lauraceae) tree located on sandbar in the middle of a river in Amazonian Brazil. The sandbar would have been underwater during rains. The floor was littered with remains of beetles.

Considerable energetic savings are made by forming monospecific roosts and roost selection and group interaction are both important aspects of the natural history of the species. Though individual bats may occasionally use other roosts they are typically faithful to a main roost, and during a study in Costa Rica seven radiotracked bats returned to the main roost on 51 of the 55 days they were tracked. The bats emerged from the roost c30 minutes after sunset. Time away from the roost is almost entirely dedicated to foraging activity and the species averaged 117.6min/night (+/- 81.2min) away from the roost during the same study. (Fenton et al 1993).

**Mortality** Dunn (1933) reported captive individuals being consumed by the predatory bat *Phyllostomus hastatus*, but no records of this occurring under natural conditions exist.

**Parasites** Pressley & Willig (2008) noted that total ectoparasite abundance increased with size in this species in Paraguay. Presley (2005) found 1460 parasites on 68 specimens of this bat in Paraguay, including two streblids (*Noctiliostrebla maai* and *Paradyschiria parvula*), a chirodiscid (*Lawrenceocarpus* sp.), and an argasid (*Ornithodoros basei*). Both streblids were monoxenous. Dick & Gettinger (2005) found the following Streblids on this species in Paraguay with prevalences given as number of individuals affected out of total number captured, followed by total number of parasites: *Noctiliostrebla maai* (45 of 67; 213), *Paradyschiria parvula* (61 of 67; 434) and *Xenotrichobius noctilionis* (6 of 67; 6).

Mites (Acari): *Parakosa tadarida*, *P.maxima* in Nicaragua. *Mitonyssus* sp. in Venezuela, Surinam and Bolivia. *Mitonyssus noctilio* was to be considered restricted to this species by Yunker & Radovsky (1980). Tick (Argasidae): *Ornithodoros basei*. Bat Flies (Streblidae): *Paradyschiria parvula*, *P.parvuloides*, *Noctilionstrebla aitkeni*, *N.maai*. The latter genus is found only on bats of this family (Wenzel et al 1966).

**VOCALISATIONS:** Echolocation begins with uniform cries of 70kHz which modulate down to 40kHz after several milliseconds. Repetition rates as high as 200s have been recorded when pursuing food. (Hood & Pitocchelli 1983).

Kalko et al (1998) associated echolocation calls with foraging strategies in Costa Rica and Panama (see foraging behaviour and diet for behaviours associated with these calls):

1) *High Search Flight* Groups of two or three constant frequency (CF) or constant frequency-frequency modulated (CF-FM) signals of medium duration (10ms) emitted near the top of each wing beat. In double-pulse groups the first pulse is usually a CF signal and the second a mixed CF-FM signal. Groups with more pulses consisted of a mixtures of all signal types, though usually ended with a CF-FM signal. Typically when foraging high over land (though occasionally in other scenarios) long FM calls with varying sweep rates were emitted. FM signals are longest (17-21ms), followed by CF-FM and CF signals (10.11ms). In CF-FM signals the two components are of roughly equal length and the interval between the last signal of a group and the first signal of the next group was approximately 70-210ms, 2-4 times the interval between signals within a group (30-50ms). The amount of time filled with sound (duty cycle) varied from 5-7% between signal groups to >30% within signal groups. CF signals began with a 1.2ms upward modulation of 0.4-1kHz, followed by a constant middle portion of 0.4kHz and ending in a short, 2-3ms downward-modulated portion of 2-4kHz bandwidth. The CF component of CF-FM signals was similar. CF-FM signals ended in a 5ms downward FM sweep and a bandwidth of 32kHz. During the approach sequence the pulse duration and pulse interval were reduced, the CF component of the signals being reduced and eventually dropped. Just prior to capture a series of short FM signals (2ms) were uttered at a high repetition rate (160-180Hz), and it was only during this terminal phase that emitted signals overlapped those returning from the prey. Signals ceased 15-20cm from contact, with the duty cycle rising from 19-30% during the search phase to 40-45% in the terminal phase. Following capture they return to the search phase after a pause of 90.2ms (+/-64.4ms, range 18.1-180.3ms).

2) *Low Search Flight* Signal pattern differed dramatically from High Search Flight with long series of short CF-FM pulses interspersed with groups of longer signals, usually a CF signal followed by 2-4 CF-FM signals. Pulse duration was also much lower (6.5 vs 10.9ms). Duration of CF signals and FM components, as well as FM bandwidth were similar to those of High Search Flight. Short CF-FM signal groups resembled approach phase signals and pulse interval varied from 10 to >100ms. Intragroup and intergroup intervals were shorter than in High Search Flight. In short CF-FM signal groups, intragroup intervals ranged between 10-30ms. Between groups of short CF-FM signals or longer CF and CF-FM signals intergroup interval was 40-70ms. Duty cycle was 28%, much higher than in High Search Flight and oscillating between 10-40%. Signal emission was correlated with wing beat, with groups of short CF-FM signals and longer CF and CF-FM signals corresponding to one wing beat cycle.

3) *Overland Tactics* Similar to High Search Flight over water though bats foraging overland frequently emitted long FM signals (17-21ms). Long FM signals began with a short (3-4ms), steep (7-10kHz/ms), downward FM sweep, levelling out in a shallow-modulated (c1kHz/ms) component of 10-12ms. The signal ended with a steep (10-12 kHz/ms) downward sweep c1ms in duration.

Brown et al (1983) studied the echolocation behaviour of this species in wild and captive scenarios in Panama. They noted that prey was captured using a combination of constant and frequency-modulated pulses and while flying over water searching for prey that they frequently alternate constant frequency narrow band frequency modulated signals with constant frequency wide band frequency modulated signals. Upon approaching an object an almost pure frequency-modulated pulse is given. The constant frequency component was between 65-75kHz, differing from that of *N.leporinus* (55-65kHz) and meaning that the two species can be distinguished in the field through their sonar signals.

Juveniles give long frequency-modulated "isolation calls" and shorter mixed constant/frequency-modulated pulses (duration c 10ms) which are recognised individually by the mother. The short mixed calls are likely the precursors to echolocation and were given when crawling, the longer "isolation calls" were given in response to stress or isolation. A great variety of calls are given by newborns, but within a week they begin to stabilise into a predictable form. Initially juvenile bats cry almost continuously and mothers respond with long frequency-modulated sinusoidal signals, but by 2 weeks of age the juvenile crawls towards its mother with a mutual exchange of vocalisations. Calls eventually evolve into adult like calls as the constant frequency component increases in frequency (from 40kHz at birth to 65kHz at 1 month) and the repetition rate increases.

When a young bat begins to fly it gives repeated short series of staccato pulses at a high repetition rate, these becoming less frequent over the course of the first week when pulses become more adult like, with increased repetition rates during take-off, landing and avoidance of obstacles only. Mother-young pairs also apparently duet when on the wing, giving constant frequency and short frequency-modulated signals. Adults also apparently produce an enormously diverse and complex array of communication sounds.

**HUMAN IMPACT:** Human impact likely negligible, and the species may even be benefitting from damming schemes along the Rio Paraná which are creating more suitable habitat and allowing its expansion east. Considered a bioindicator of water quality in the Ecuadorian Amazon by Tirira (1994).

**CONSERVATION STATUS:** Globally considered to be of Least Concern by the IUCN, see <http://www.iucnredlist.org/search/details.php/14829/all> for the latest assessment of the species. Considered stable and common in Paraguay in areas of suitable habitat (López-Gonzalez 2005) and possibly more widespread than currently thought. This species adaptability, its tolerance of human activity and its preference for large watercourses with slow-moving currents means that it may even be expanding its range as damming schemes along the Rio Paraná tame the previously rapid-flowing river and open up new opportunities for colonisation. There are only three records of the species in Misiones, Argentina and Massoia et al (2006) considered it rare in the province. Following extensive sampling in Paraguay, Willig et al (2000) found this species to account for 3.37% of all bats caught in the Pantanal region, 9.25% of those in the Humid Chaco, 0.34% in the cerrado and 12.18% in Ñeembucú (n=3989).

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**FIGURE 2** - (FPMAM102PH) **Lesser Bulldog Bat** *Noctilio albiventris*. Photo Silvia Centrón. Adult head detail brown phase. Bahía Negra, Departamento Alto Paraguay, September 2009.  
**FIGURE 3** - (FPMAM103PH) **Lesser Bulldog Bat** *Noctilio albiventris*. Photo Silvia Centrón. Adult head detail brown phase. Bahía Negra, Departamento Alto Paraguay, September 2009.



**FIGURE 4** **Lesser Bulldog Bat** *Noctilio albiventris*. Head detail orange phase. (© Merlin D. Tuttle, Bat Conservation International, www.batcon.org).  
**FIGURE 5** **Lesser Bulldog Bat** *Noctilio albiventris*. Head detail orange phase. (©Marco Mello www.casadosmorcegos.org).



**FIGURE 6** - (FPMAM105PH)  
**Lesser Bulldog Bat** *Noctilio albiventris*.  
 Guano pile. Pozo Colorado, Departamento Presidente Hayes, October 2008.  
 Photo Paul Smith.





**FIGURES 7-12** - Skull (©Philip Myers/Animal Diversity Web <http://animaldiversity.ummz.umich.edu>).