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The Taxonomic Status of *Lasiurus* (Chiroptera: Vespertilionidae) in the Galapagos Islands

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ABSTRACT

Morphological comparisons of the endemic Galapagos bat *Lasiurus brachyotis* with related taxa indicate that *L. brachyotis* should be recognized as a subspecies of *L. borealis*. Morphology suggests that other recognized taxa of the *L. borealis*

group, including *blossevilli*, *degelidus*, *frantzii*, *minor*, *pfeifferi*, *seminolus*, *teliotis*, and *varius* are members of the same species. Specimens of the only other bat inhabiting the Galapagos are allocated to *Lasiurus cinereus villosissimus*.

INTRODUCTION

Only two species of bats are known from the Galapagos, both referable to the widespread American genus *Lasiurus*. The first was described as a separate species, *L. (Atalapha) brachyotis*, from a single specimen collected in 1891 on the Island of San Cristobal (Allen, 1892). Prior to the report of McCracken et al. (1997), the only other reports of *brachyotis* were from skeletal remains in owl pellets, including a skull col-

lected from Santa Cruz (Niethammer, 1964) and the remains of at least 11 individuals from Floreana (Steadman, 1986). McCracken et al. (1997) recorded *brachyotis* on San Cristobal and Santa Cruz and obtained five specimens, one male and one female collected on each island and a partially decomposed specimen from Santa Cruz (AMNH 268073-7). There was no evidence for the presence of *L. brachyotis* on three

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other islands, including Floreana (McCracken et al., 1997).

Until 1964, *L. brachyotis* was the only species of bat known from the Galapagos, but in that year, Niethammer (1964) recorded *L. cinereus* from Santa Cruz along with *brachyotis*. Prior to that, sight records of bats from the Galapagos (Allen, 1892; Brosset, 1963; Brosset and de Beaufort, 1963) were assumed to be *L. brachyotis*, though some were almost certainly *L. cinereus*. *Lasiurus cinereus* was not known from any other Galapagos islands, although Orr (1966) and Peterson (1966) recorded additional specimens from Santa Cruz. McCracken et al. (1997) reported *cinereus* on five islands (Santa Cruz, San Cristobal, Floreana, Isabela, and Santiago) and collected three specimens, a male and a female from Santa Cruz and a male from Isabela (AMNH 268078-80).

Noting its morphological similarity to *L. cinereus villosissimus* of mainland South America, Peterson (1966) placed Galapagos *L. cinereus* in that subspecies. Except for Allen's (1892) brief description, nobody, as far as we know, has compared Galapagos *L. brachyotis* with related populations. In order to determine the correct taxonomic allocation of the Galapagos *Lasiurus* populations, we have examined the specimens of both species that were collected by McCracken et al. (1997). The relatively simple case of *L. cinereus* will be taken up first, then the more complex one of the *L. borealis* group to which *brachyotis* belongs.

Lasiurus cinereus

The subspecies of *L. cinereus* were reviewed by Sanborn and Crespo (1957), who recognized three subspecies but saw no Galapagos specimens. Protein electrophoretic and DNA sequence data (Baker et al., 1988; Morales and Bickham, 1995), which also did not include the Galapagos forms, are consistent with the recognition of three subspecies of *L. cinereus*. Here we compare *L. cinereus* from the Galapagos with material of all three subspecies in the collections of the American Museum of Natural History and the Field Museum of Natural History. *Lasiurus c. cinereus* of North America is relatively large (condylobasal length of skull 16.3–17.3

mm). It is dark gray in color with variable amounts of frosting, often heavy. *Lasiurus c. semotus* of the Hawaiian Islands is smaller (condylobasal length 14.8–16.0 mm) and shows great variation in both basal color (reddish brown to dark brown) and the amount of frosting (none to heavy). *Lasiurus c. villosissimus* of South America is also relatively small (condylobasal length 14.7–16.0 mm) and likewise shows great color variation. Specimens from northern and central South America (Venezuela, Colombia, Peru, Bolivia, and Paraguay) are definitely brown in basal coloration; most from Uruguay and Argentina, and apparently all from Chile, are darker and grayer, thus approaching *L. c. cinereus*. However, all South American specimens tend to be only lightly frosted. This color variation suggests geographical variation within South America, but the interpretation is complicated by seasonal migration that occurs in both South and North America (Sanborn and Crespo, 1957; Findley and Jones, 1964). Although it is possible that more than one subspecies could be recognized in South America (there are three available names), we prefer at present to follow Sanborn and Crespo (1957) in referring all South American specimens to *L. c. villosissimus*. Galapagos specimens are light to medium gray and relatively small (condylobasal length 14.4–16.2 mm); thus they fall into the range of variability of *L. c. villosissimus*. If all South American mainland specimens are allocated to *villosissimus*, we agree with Peterson (1966) that Galapagos specimens can best be referred to the same subspecies.

Lasiurus (borealis) brachyotis

Handley (1960) reviewed the *L. borealis* group and recognized the following as subspecies: *b. borealis* (eastern North America), *b. frantzii* (Central and northern South America), *b. teliotis* (western United States and most of Mexico), *b. blossevillii* (southeastern South America), and *b. varius* (Chile). *Lasiurus castaneus* (Panama), *L. egregius* (Brazil), and *L. seminolus* (southeastern United States) were recognized as regionally endemic species. No mention was made of *brachyotis* (Galapagos) or of the three West Indian

members of the group: *degelidus* (Jamaica), *pfeifferi* (Cuba), and *minor* (Hispaniola and the Bahamas). On the basis of electrophoretic studies of six of these taxa (*borealis*, *blossevillii*, *seminolus*, *teliotis*, *frantzii*, and *degelidus*), Baker et al. (1988) recognized *borealis*, *blossevilli*, *seminolis*, and *degelidus* as separate species and *teliotis* and *frantzii* as subspecies of *blossevillii*. DNA sequence data (Morales and Bickham, 1995) corroborated Baker et al.'s (1988) designations of *borealis*, *blossevillii*, and *seminolus* as species. Morales and Bickham (1995) also recognized *pfeifferi* as a species and suggested that *L. blossevilli teliotis* of western North America and Mexico and *L. blossevillii blossevillii* of South America (as recognized by Baker et al., 1988) might warrant species status. This latter recognition was tentative due to the uncertain status of *frantzii*.

Specimens of all of these taxa have been examined from the collections of the American Museum of Natural History, the U.S. National Museum, and the Field Museum of Natural History. We would exclude *egregius* from the *borealis* group on the basis of its much larger size, the absence of an anterior upper premolar (although as Handley [1960] pointed out, this premolar may be occasionally absent in the *borealis* group as well, as it was in 1 of 40 Neotropical *borealis* group skulls we checked), and a less-reduced ear pinna (a character that Handley did not mention). In our opinion, *egregius* is better placed with the *ega-intermedius* group in the subgenus *Dasypterus* that we would recognize.

Of the above-listed taxa, *castaneus* is clearly distinct from the rest in its more shortened rostrum and very high braincase with the occipital condyles raised above the basicranium. We have seen no specimens of two recently described species belonging to the *borealis* group: *ebenus* Fazzolari-Corrêa (1994) from southeastern Brazil and *atratus* Handley (1996) from Venezuela and the Guianas. From their descriptions, both seem rather distinct from other members of the group.

Further comparisons contrasting the core members of the *borealis* group (*borealis*, *seminolus*, *teliotis*, *frantzii*, *blossevillii*, *varius*, *degelidus*, *pfeifferi*, *minor*, *brachyotis*),

which hereafter will be referred to as the *borealis* complex, involved a series of skin and skull characters (table 1). Here we summarize those comparisons. Specimens of *brachyotis* are gray in color with little red, differing from all forms examined except perhaps some specimens of *blossevillii* and *minor*. Hair on the dorsal side of the uropatagium of *brachyotis* is similar to that of some South American taxa but also to that of the island taxa *minor* and *pfeifferi*. Condylbasal length of the skull of *brachyotis* is most similar to that of *varius* of Chile but is not very different from other taxa (e.g., *borealis*, *seminolus*, and *pfeifferi*). The lacrymal tubercle is poorly developed in *brachyotis*, the other island taxa (*degelidus*, *pfeifferii*, and *minor*), and *seminolus*. It is generally well developed in nominate *borealis* and *blossevilli* and variably developed in the other mainland taxa. Related to the lacrimal tubercle is the size of the infraorbital foramen, which lies anteroventral to the lacrimal tubercle, the two separated by a bridge of bone. In most members of the *borealis* complex, this foramen is very small (much less than the diameter of the upper incisor), but in *brachyotis* it is enlarged (about the same as the diameter of the upper incisor).

From our morphological examinations we find little basis for recognizing more than one species in the *borealis* complex. Of course, there is broad overlap in the overall ranges of nominate *borealis* and *seminolus*, and a specimen referable to *teliotis* has been recorded (Genoways and Baker, 1988) from Trans-Pecos Texas, otherwise inhabited by nominate *borealis*. However, Koopman (1983) has pointed out that sympatry outside the time of mating is not evidence for species status, and sympatry at the time of mating is not easy to determine in migratory bats. Indeed, the *borealis*-*seminolus* case was one of the examples discussed by Koopman (1983). Also, Schmidly and Hendricks (1984) have documented apparent intergradation between *teliotis* and nominate *borealis* in Tamaulipas, northeastern Mexico. In short, it has not been demonstrated that sympatry at the time of mating exists between any two members of the *borealis* complex, and we are inclined to treat all members as subspecies of *L. borealis*. Although it could be argued that

TABLE 1
Skin and Skull Characteristics of Members of the *Lasius borealis* Species Complex

Taxon	Color of dorsal fin	Hair on dorsal side of uropatagium	Condylobasal length of skull (mm)	Lacrimal tubercle
<i>blossevillii</i>	Brick red to grayish; more gray on females	Typically sparsely haired posteriorly	10.5–12.6	Generally well developed
<i>borealis</i>	Brick red to almost mahogany; typically more white frosting on females	Completely haired	12.1–13.2	Well developed
<i>brachyotis</i>	Grayish brown with little red; virtually no sexual dimorphism	Somewhat sparsely haired posteriorly	12.4–13.4	Poorly developed
<i>degeidus</i>	Not examined	Not examined	13.4 (only one specimen measured)	Poorly developed
<i>frantzii</i>	Light red to brick red; typically little sexual dimorphism	Somewhat sparsely haired posteriorly (completely haired on Pearl Islands, Panama)	10.5–11.7 (except in western Ecuador, where 11.9–12.1)	Variably developed
<i>minor</i>	Brick red to grayish brown; little sexual dimorphism	Somewhat sparsely haired posteriorly	12.1 (only one intact skull measured)	Poorly developed
<i>pfeifferi</i>	Brick red on one male examined, no females examined	Somewhat sparsely haired posteriorly	12.6–13.0	Poorly developed
<i>seminolus</i>	Deep mahogany; no sexual dimorphism	Completely haired	12.1–13.1	Poorly developed
<i>telionis</i>	More or less brick red; typically more white frosting on females	Usually completely haired, sparsely haired posteriorly on some	11.5–12.9	Variably developed
<i>varius</i>	Deep red; no sexual dimorphism	Completely haired	12.4–13.4	Variably developed

brachyotis deserves species recognition because it is as distinct as other taxa that have been considered species (*seminolus*, *pfeifferi*, *minor*, *blossevillii*, and *degelidus*), it seems to us that *brachyotis* is best considered one of the better-differentiated subspecies in the *bo-realis* complex.

Lasiurus b. frantzii is the subspecies that occurs closest to the geographic range of *brachyotis*, apparently occupying the entire Pacific side of tropical America from Guatemala to Peru, including the Pacific side of Ecuador. However, *brachyotis* differs from *frantzii* in being much duller in color (virtually no red), being considerably larger in size (no overlap in condylocanine length), having the lacrimal tubercle always poorly developed, and having the infraorbital foramen enlarged. It is interesting, however, that the largest specimens of *frantzii* are from western Ecuador, the coast opposite the Galapagos. If the ancestors of *brachyotis* came from this area, as seems reasonable, then the larger size of the *frantzii* from western Ecuador may be significant. Chile is another

possible site of origin for bats colonizing the Galapagos. Whereas *brachyotis* differs from *varius* of Chile in fur characteristics, *brachyotis* and *varius* are similar in size and lacrimal tubercle development.

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