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GENIC VARIATION OF MAINLAND AND ISLAND POPULATIONS OF *NATALUS STRAMINEUS* (CHIROPTERA: NATALIDAE)

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The funnel-eared bats, *Natalus stramineus*, occur on the continental Americas from northern México to Venezuela and eastern Brazil and throughout the Antilles (Koopman, 1993). Beginning with the description of *Natalus*, the taxonomic history of the genus has been characterized by a degree of confusion, with few systematic studies and no phylogenetic analysis (Handley and Gardner, 1990). Based on a comprehensive study of several morphologic characters, Dalquest (1950) relegated two of the four recognized genera (*Chilonatalus* and *Nyctiellus*) of the family Natalidae to subgeneric status and placed a third genus (*Phodotes*) within the subgenus *Natalus*. In addition, Dalquest (1950) reviewed the available literature and recognized six species within the subgenus *Natalus* (*N. stramineus*, *N. mexicanus*, *N. major*, *N. dominicensis*, *N. primus*, and *N. tumidirostris*).

Cabrera (1975) agreed with the inclusion of *Phodotes* within *Natalus* and the relegation of *Chilonatalus* to subgeneric status. However, without explanation, he retained specific status only for *N. tumidirostris* and synonymized the remaining five species of the subgenus *Natalus* with *N. stramineus*. Hall and Kelson (1959) considered the genus *Natalus* to be comprised of the three subgenera proposed by Dalquest (1950); however, *N. stramineus* was not mentioned to

occur in either North America, Central America, or the Antilles. Instead, the subgenus *Natalus* was considered as including *N. mexicanus*, *N. dominicensis*, and *N. primus*.

Goodwin (1959) reviewed the three species he considered to compromise the subgenus *Natalus* (*N. stramineus*, *N. major*, and *N. tumidirostris*) and proposed the naming of three new subspecies (*N. stramineus natalensis*, *N. major jamaicensis*, and *N. tumidirostris haymani*). Moreover, Goodwin (1959) and Baker and Jordan (1970) noted the close relationship of *N. tumidirostris* to *N. stramineus*. Based on comparisons of the palate, Linares (1971) proposed two groups within the subgenus *Natalus*; the *N. stramineus*/*N. major* group (characterized by a very short palate) and the *N. tumidirostris* group (characterized by a long palate). Linares (1971) assigned the subspecies *N. stramineus major* with *N. stramineus mexicanus*. Linares (1971) proposed that *N. tumidirostris* could be included with *N. stramineus*, if further support could be provided for the possible cline that he detected for *N. stramineus* and *N. major* with respect to palatal length.

Varona (1974) concluded that the Caribbean bats of the subgenus *Natalus* comprised only two species,

N. micropus (which included *N. macer* and *N. tumidirostris*) and *N. stramineus* (which included *N. major*). However, Hoyt and Baker (1980) considered *N. major* to be easily distinguished from *N. stramineus* and retained specific status for *N. major*. Hall (1981) followed Varona's (1974) proposal for the family Natalidae, recognizing six subspecies of *N. stramineus* (including *N. stramineus major*, *N. stramineus mexicanus*, and *N. stramineus saturatus*). Honacki et al. (1982) recognized four species within the family (*N. stramineus*, *N. lepidus*, *N. micropus* and *N. tumidirostris*), whereas Corbet and Hill (1991) and Koopman (1993), without providing data to support their proposals, listed five species for the genus (the four recognized by Honacki et al. 1982 and *N. tumidifrons*).

Few studies utilizing characters other than morphology have been used to evaluate the systematic relationship within the genus *Natalus*. Kerridge and Baker (1978) described the karyotype of *N. micropus* and suggested that contrary to the conclusion of Baker and Jordan (1970), the standard karyotypes of three species (*N. micropus*, *N. stramineus*, and *N. tumidirostris*) exhibited some detectable differences. Of the three karyotypes, the two that most closely resemble one another are those of *N. micropus* and *N. stramineus*, being indistinguishable or differing by the amount of material composing the shortest arm of the smallest banded element. The karyotype of *N. tumidirostris* differs from those of the previous two species in having a medium-sized pair of subtelocentric elements, whereas the smallest pairs of banded elements in *N. tumidirostris* do not appear closely comparable in relative size with those of the other two species. At present, no published study using either banded chromosomes or genic data exists for determining the relationships within the genus *Natalus*.

The need exists for further systematic study of *N. stramineus*. Based primarily on morphologic characters, there are several problems to resolve, including the validity of the several proposed taxonomic names. Moreover, the relationship of *N. major* to mainland and insular populations of *N. stramineus* remains unclear (Baker and Genoways, 1978). This study focuses on the genic variation of specimens assigned to the complex of taxa presently considered within the single species, *N. stramineus*, from the mainland and the Antilles. Of particular interest, it is a determination of the specific status of *N. major*.

METHODS AND MATERIALS

Specimens were collected using both mist and hand nets. Mainland populations of *Natalus stramineus* are those from México and Belize; those from Dominica (Lesser Antilles) are considered to represent the type subspecies.

Immediately following sacrifice, samples of liver, kidney, and heart were removed and frozen in liquid nitrogen. Methods for tissue preparation, starch-gel electrophoresis, and enzyme designations were similar to those of Selander et al. (1971) and Harris and Hopkinson (1976). The following enzymes encoded by 34 presumptive loci (abbreviations in parentheses) were examined: aspartate amino-transferase (AAT-1, AAT-2); aconitase (ACON-1, ACON-2); adenylate kinase (AK-1, AK-2, AK-3, AK-4); creatine kinase (CK-1, CK-2, CK-3); esterase-naphthyl propionate (EST-1, EST-2); glucose phosphate isomerase (GPI-1, GPI-2); hexokinase (HK-1, HK-2); isocitrate dehydrogenase (ICD); lactate dehydrogenase (LDH-1, LDH-2); malate dehydrogenase (MDH-1, MDH-2); malic enzyme (ME); mannose phosphate isomerase (MPI-1, MPI-2); nucleoside phosphorylase (NP); peptidase-B (PEPB: Leucyl-Glycyl-Glycine); phosphoglucosmutase (PGM-1, PGM-2, PGM-3); 6 phosphoglucosmutase dehydrogenase (6-PGD); sorbitol dehydrogenase (SORD); xanthine dehydrogenase (XDH). Loci were designated numerically with "1" being the most anodally migrating isozyme of the enzyme, and the more cathodally migrating isozymes being designated by increasingly larger number. In naming allelic differences for polymorphic loci, the most common allele was designated as "100," and all additional alleles were assigned numeric values according to their mobility relative to the most common allele.

To determine genetic similarity between taxa, Rogers' (1972) and Nei's (1972) genetic distance coefficients were calculated. From the matrix of Nei's genetic distance, an unweighted pair-group method using arithmetic averages (UPGMA) cluster analysis was performed using PHYLIP (Felsenstein, 1991). To evaluate phylogenetic relationships, all alleles were coded as discrete characters and analyzed using PAUP, version 3.0 (Swofford, 1991). Polarization of character-state changes was established by designation *N. micropus* as the out group. The most parsimonious tree was searched for using the Exhaustive search option of PAUP

with the reliability of the resulting clades determined via a bootstrap analysis with 1,000 iterations and the Branch-and-Bound option (Felsenstein, 1985).

Frozen tissue samples and voucher specimens are deposited at the Texas Cooperative Wildlife Collection, Texas A&M University (AK/TCWC), the Museum of Southwestern Biology, University of New Mexico (NK/MSB), the Carnegie Museum of Natural History (CM), and the Museum of Texas Tech University (TK/TTU).

Material examined.— St. Claire Cave, St. Catherine Parish, Jamaica, 10 specimens of *Natalus micropus* (TK 9446-9455/CM 44570-44579); 11 specimens of *Natalus stramineus major* (TK 9421-9431/TTU 29110-29120). Santo Domingo Mine at La Aduana, 3 mi S, 2.8 mi W of Alamos, Sonora, México, seven specimens of *Natalus stramineus mexicanus* (NK 5633/MSB 53772, 5635/53766, 5637/53773, 5638/53768, 5641/53746, 5645/53770, 5646/53777). 0.75 km W of Augustine, Belize, one specimen of *Natalus stramineus saturatus* (AK 7755/CM 91910). Richmond Hill (Goat Hill) in Orange Walk District, 8.9 km SSW of Orange Walk Town, Belize, one specimen of *Natalus stramineus saturatus* (AK 7765/CM 91917). Gruta de Balankanchén, 5 km E of Chichén-Itzá, Yucatán, México, two specimens of *Natalus stramineus saturatus* (ASK 435/ASNHC 2500; 437/ Cat. no. n/a). Springfield, St. Paul Parish, Dominica, one specimen of *Natalus stramineus saturatus* (TK 15579/TTU 31486). 0.5 mi N of Toucari, St. John Parish, Dominica, nine specimens of *Natalus stramineus stramineus* (TK 15648/TTU 31464, 15650/31472, 15652/31474, 15654/31476, 15655/31477, 15657/31479, 15658/31480, 15659/31481).

RESULTS

Of the 34 presumptive loci examined, 14 were monomorphic with all samples fixed for the same allele. Allelic frequencies of the 20 variable loci (frequency of the common allele in at least one population less than 0.99) are shown in Table 1. Nei's (1972) and Rogers' (1972) genetic distance values for all pairwise comparisons are presented in Table 2. As can be seen from this table, the pairwise distance of *N. micropus* is approximately twice the distance between any two taxa of the *N. stramineus* complex. Additionally, *N.*

stramineus from Jamaica and Dominica, as well as those populations from México and Belize, are the most similar. Within *N. stramineus*, the highest levels of genetic difference are found when populations from the Yucatán peninsula of México are compared with populations from either Jamaica or Dominica.

Phenetic relationships for these taxa based on Nei's (1972) genetic distance values are summarized in Figure 1. Two large groups are detected representing populations from the mainland (northern México, southern México, and Belize) and the Caribbean islands (Jamaica and Dominica). Populations of *N. stramineus* from northern México are phenetically closer to specimens from Belize than they are to specimens from geographically closer southern México. This also is true in one of the two most parsimonious trees from the phylogenetic analysis.

The phylogenetic analysis resulted in two most parsimonious trees of 59 steps (CI=0.847). Figure 2 is the resultant topology from the bootstrap analysis using the Branch-and-Bound algorithm. The topology of the other most parsimonious tree differed from that shown in Figure 2 by placing the specimens from Belize as sister to the populations from southern México. As with the phenetic analysis (Fig. 1), parsimony analysis documents that populations of *N. stramineus* from the mainland are more closely related to each other than they are to populations from Caribbean islands. Populations of *Natalus* from Jamaica (*N. stramineus jamaicensis* and *N. micropus*) appear to be equally distant from all other populations examined in this study (Fig. 2).

DISCUSSION AND CONCLUSIONS

Natalus stramineus has long been considered as having populations in both mainland America and the West Indies. However, there have been different suggestions as to the taxonomic status of the island populations, either within *N. stramineus* or as a distinct species, such as *N. major* (cf. Varona, 1974; Hoyt and Baker, 1980). Likewise, it has been debated whether mainland populations of *N. stramineus* occurring in North and Central America pertain to one (*N. stramineus mexicanus*) or two subspecies (*N. stramineus mexicanus* and *N. stramineus saturatus*).

Table 1. Allele frequency of the 20 variable loci for *Natalus micropus* and the five populations of *N. stramineus*. See text for locus abbreviations.

Locus	Allele	<i>N. micropus</i> n = 10	Jamaica n = 10	Dominica n = 10	Belize n = 2	N. México n = 7	S. México n = 2
AAT-1	200	1.00	0.00	0.00	0.00	0.00	0.00
	175	0.00	0.00	0.00	1.00	0.57	1.00
	150	0.00	0.00	0.00	0.00	0.29	0.00
	100	0.00	1.00	1.00	0.00	0.14	0.00
Acon-1	100	0.80	1.00	1.00	1.00	1.00	1.00
	90	0.20	0.00	0.00	0.00	0.00	0.00
Acon-2	105	0.00	0.00	0.10	0.00	0.00	0.00
	100	0.00	1.00	.90	1.00	1.00	1.00
	90	0.70	0.00	0.00	0.00	0.00	0.00
AK-2	10	0.30	0.00	0.00	0.00	0.00	0.00
	110	1.00	0.00	0.00	0.00	0.14	0.00
	100	0.00	1.00	1.00	1.00	0.86	1.00
AK-3	100	0.00	1.00	1.00	1.00	1.00	0.00
	N	1.00	0.00	0.00	0.00	0.00	1.00
EST-2	130	0.00	0.00	0.00	1.00	1.00	1.00
	120	0.00	0.00	0.10	0.00	0.00	0.00
	110	0.05	0.25	0.00	0.00	0.00	0.00
	100	0.95	0.75	0.00	0.00	0.00	0.00
GPI-1	105	0.00	0.00	0.00	0.00	0.14	1.00
	100	0.00	1.00	1.00	1.00	0.86	0.00
	95	1.00	0.00	0.00	0.00	0.00	0.00
GPI-2	100	0.00	1.00	1.00	1.00	1.00	1.00
	-5	1.00	0.00	0.00	0.00	0.00	0.00
HK-1	105	0.00	0.00	0.00	0.00	0.00	0.00
	100	0.00	1.00	1.00	1.00	1.00	0.00
	95	1.00	0.00	0.00	0.00	0.00	0.00
ICD	110	0.00	0.00	0.00	0.00	0.00	0.50
	100	1.00	1.00	1.00	1.00	1.00	0.50
LDH-2	110	0.80	0.00	0.00	0.00	0.00	0.00
	100	0.20	1.00	1.00	1.00	1.00	1.00
	ME	105	1.00	0.00	0.00	0.00	0.00
MPI-1	100	0.00	1.00	1.00	1.00	1.00	1.00
	5	1.00	0.00	0.00	0.00	0.00	0.00
MPI-2	120	0.00	0.00	0.00	1.00	0.29	1.00
	110	0.00	0.00	1.00	0.00	0.71	0.00
	105	1.00	0.00	0.00	0.00	0.00	0.00
	100	0.00	1.00	0.00	0.00	0.00	0.00
NP 210	0.00	0.00	0.00	0.00	0.00	0.50	
	200	0.00	1.00	0.00	0.00	0.33	0.00
	150	0.00	0.00	1.00	1.00	0.67	0.50
PEP-B	100	1.00	1.00	1.00	1.00	0.86	1.00
	85	0.00	0.00	0.00	0.00	0.14	0.00
PGM-2	115	0.00	0.00	0.00	1.00	0.71	1.00
	110	0.00	0.00	0.00	0.00	0.29	0.00
	100	0.00	1.00	1.00	0.00	0.00	0.00
PGM-3	N	1.00	0.00	0.00	0.00	0.00	0.00
	125	0.00	0.00	0.00	0.00	0.50	0.00
	115	0.00	0.00	0.00	1.00	0.50	1.00
6-PGD	110	1.00	0.00	0.00	0.00	0.00	0.00
	100	0.60	1.00	1.00	1.00	1.00	1.00
XDH	90	0.40	0.00	0.00	0.00	0.00	0.00
	105	0.00	0.00	0.00	0.00	0.14	0.00
	100	1.00	1.00	1.00	1.00	0.86	1.00

Table 2. Coefficients of genetic variation for all pairwise comparisons between *N. micropus* and the populations of *N. stramineus* from the five geographic localities examined. Nei's (1972) genetic distance is given above the diagonal while Rogers' (1972) genetic distance is given below the diagonal.

Locus	<i>N. micropus</i>	Jamaica	Dominica	Belize	N. México	S. México
<i>N. micropus</i>	—	0.557	0.598	0.603	0.561	0.617
Jamaica	0.439	—	0.087	0.195	0.154	0.277
Dominica	0.460	0.089	—	0.131	0.082	0.225
Belize	0.463	0.179	0.127	—	0.071	0.080
N. México	0.448	0.175	0.120	0.112	—	0.136
S. México	0.474	0.251	0.218	0.091	0.174	—

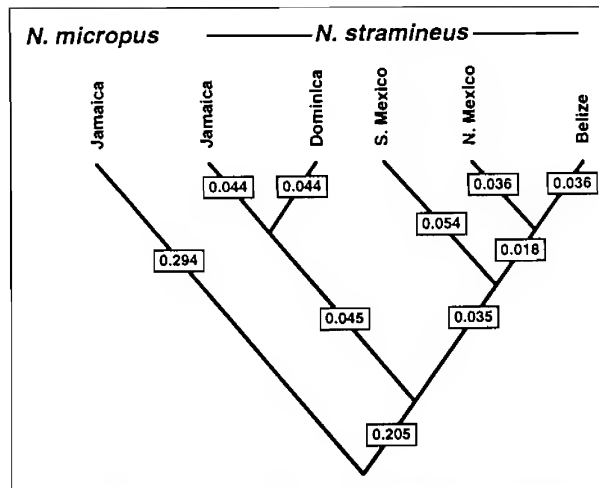


Figure 1. Dendrogram illustrating the phenetic relationships among the populations of *N. stramineus* and *N. micropus* examined in this study. This dendrogram is resultant from a UPGMA based on Nei's (1972) genetic distances values of the 34 presumptive loci assayed. Numbers in boxes along each lineage are the distance values.

The allozymic data from the populations of *N. stramineus* examined in this study provide some resolution of the phylogenetic relationships within *N. stramineus*. However, the number of characters and the sample sizes from some of the populations on which the tree is based are low (Table 1). Even with the low number of characters, some confidence can be placed on the branching patterns depicted in Figure 2. The highest confidence branching sequences in this study can be placed on the grouping of the populations of *N. stramineus* from Belize and northern and southern México, which occurred in 83% of the 1,000 bootstrap iterations.

Hillis and Bull (1993) conducted simulation studies on bootstrap values and concluded that, in general, bootstrap values are conservative estimates of the reliability of clades. More specifically, they suggest that under equal rates of change, symmetric phylogenies, and internodal distances $\leq 20\%$ of the characters, bootstrap values of $\geq 70\%$ usually correspond to confidence limits of $\geq 95\%$. Although it is clear that the tree in Figure 2 violates the assumption of a symmetric topology, confidence is placed in the clade containing the Belizean and Mexican populations due to its high bootstrap value (83%). A second clade for which some degree of confidence exists is that which unites all populations of *N. stramineus* from the mainland with the population from

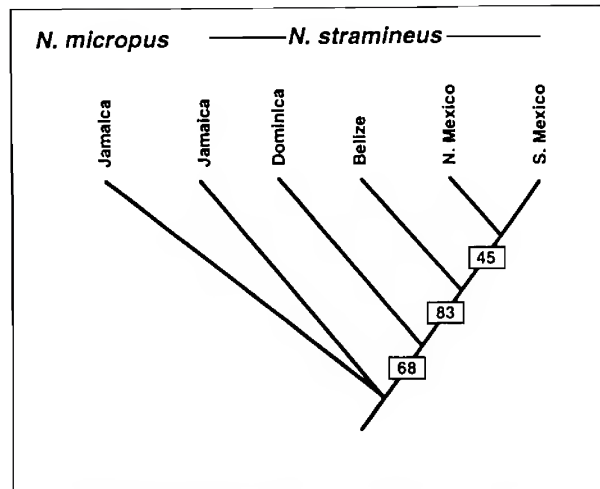


Figure 2. Topology of one of the two most parsimonious trees of 59 steps (CI=0.847) reflecting the phylogenetic relationships among the populations of *N. stramineus* examined. Numbers in boxes along the internal lineages reflect the percentage of 1,000 bootstrap iterations that each clade was detected whereas numbers along each lineage are the assigned branch lengths from PAUP.

Dominica (68%). Although this bootstrap value is clearly on the border of a 95% confidence interval, it would fall within a 90% interval, given the above stated assumptions.

This study points out the close phylogenetic relationship of the mainland populations, and a more distant relationship of the *N. stramineus*-like populations from Jamaica. Baker and Genoways (1978) proposed that Antillean islands were invaded by *N. stramineus* from South America through the Lesser Antilles, as also suggested by Koopman (1990). Moreover, Baker and Genoways (1978) proposed that *N. stramineus major* (which was considered a valid species at the time of their work) invaded the Greater Antilles through the western route, which they proposed originated on the Yucatán Peninsula. Additionally, they felt that this western route was probably the most important corridor for bat invasions of the Greater Antilles due to the ecological similarities of the Yucatán peninsula and the Antilles, as well as the close geographic proximity.

With the exception of the comparisons of populations of northern and southern México, the genetic distances among the three mainland populations are lower than when any of these populations are compared with the two island populations. The larger genetic distance

between populations from northern and southern México could be attributed to the large habitat diversity found in México where extant *Natalus* occur. Such ecological diversity could provide population subdivisions due to geographic isolation. An additional factor that could be accounting for the patterns of genetic difference between the mainland and island populations relates to the small sample sizes of individuals from the populations from southern México and Belize. Larger sample sizes could reveal different patterns of genetic difference if these populations are more variable than detected in the small sample size analyzed in this study.

Two possible explanations for the basal position of *N. stramineus* from Jamaica are: *N. stramineus* from Jamaica may actually represent a species distinct from all other populations of typical *N. stramineus* or allozymic data may not be providing adequate levels of variation to resolve the phylogenetic relationships among these populations of *N. stramineus*. As for the first proposal, the most parsimonious explanation for the relationships depicted in Figure 2 would be that little allozymic change has occurred in the Jamaican population since *N. stramineus jamaicensis* and *N. micropus* diverged from their common ancestor. Goodwin (1959) pointed out that the variation between *N. major* and *N. stramineus* was sufficiently well characterized for specific separation. Hoyt and Baker (1980) supported the specific status of *N. major* based on larger size and geographic distribution.

Concerning the second proposal, it is well known that allozymic data only reveal approximately one-third of the variation that is present in the coding region of the gene. Therefore, allozymic characters may not provide adequate resolution for phylogenetic studies of closely related taxa. Several other studies on the phylogenetic relationships of even more distantly related taxa of bats than those examined in this study have failed to produce strongly supported phylogenies. For example, Koop and Baker (1983) used allozymic variation to examine the phylogenetic relationships among six species of the phyllostomid genus *Artibeus* and detected no fixed differences among those six taxa. Along these same lines, Baker et al. (1988) examined the phylogenetic relationships among the four species of *Phyllostomus* and the one of *Phylloiderma* to determine whether *Phylloiderma* represented a valid taxon. From their allozymic data, they were able to conclude that

Phylloiderma should be included as a distinct species of *Phyllostomus*; however, their resultant topology showed an unresolved tree for all five species. Recently, the relationships for both of these examples were resolved using DNA sequence variation of the mitochondrial cytochrome-*b* gene (Van Den Bussche and Baker, 1993). Therefore, allozymic studies may not provide adequate levels of resolution for addressing phylogenetic relationships in some closely related taxa, and this may be a factor in this study.

The allozymic data are unclear relative to the relationships of *N. stramineus major* to the other taxa examined. Based on the distribution of alleles detected among the 34 presumptive loci (Table I), this study suggests that the allozymic data are conservatively interpreted as supporting subspecific recognition of populations of *N. stramineus* occurring in the Greater Antilles to which the name *N. stramineus major* applies. The validity of *N. stramineus saturatus* is questioned, but the allozymic variation in the geographic sample available for this study is insufficient to resolve the phylogenetic relationships within the species. Moreover, at three of the 34 loci (EST-2, MPI-2, and NP), the Jamaican and Dominican specimens do not share any common alleles, and it is possible that these differences may signal specific distinctiveness for the two Antillean populations.

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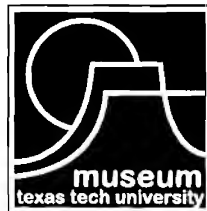
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It was through the efforts of Horn Professor J Knox Jones, as director of Academic Publications, that Texas Tech University initiated several publications series including the Occasional Papers of the Museum. This and future editions in the series are a memorial to his dedication to excellence in academic publications. Professor Jones enjoyed editing scientific publications and served the scientific community as an editor for the *Journal of Mammalogy*, *Evolution*, *The Texas Journal of Science*, *Occasional Papers of the Museum*, and *Special Publications of the Museum*. It is with special fondness that we remember Dr. J Knox Jones.

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