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TAXONOMIC STATUS OF *MYOTIS OCCULTUS*

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The taxonomic status of the Arizona myotis (*Myotis occultus*) is uncertain. Although the taxon was described as a distinct species and currently is regarded as such by some authors, others have noted what they interpreted as intergradation with the little brown bat (*M. lucifugus carissima*) near the Colorado-New Mexico state line. In this study, we used protein electrophoresis to compare bats of these nominal taxa. We examined 20 loci from 142 specimens referable to *M. occultus* and *M. lucifugus* from New Mexico, Colorado, and Wyoming. Nine of the 20 loci were polymorphic. Results show that there were high similarities among samples, no fixed alleles, and minor divergence from Hardy-Weinberg equilibrium. Our results suggest that the two nominal taxa represent only one species and that *M. occultus* should be regarded as a subspecies of *M. lucifugus*.

Key words: *Myotis occultus*, *Myotis lucifugus*, taxonomy

The nominal species *Myotis occultus*, the Arizona myotis, ranges from southeastern California eastward across Arizona to New Mexico and southward into Mexico (Hall, 1981; Miller and Allen, 1928). In New Mexico, we have observed *M. occultus* in piñon-juniper (*Pinus-Juniperus*), ponderosa pine (*Pinus ponderosa*), and cottonwood-willow (*Populus-Salix*) riparian habitats. In Arizona, Hoffmeister (1986:76) observed *M. occultus* in habitats consisting of "oak-pine woodland" and in "cottonwoods, willows, and sycamores." The related little brown myotis, *Myotis lucifugus*, is widespread across North America and consists of five recognized subspecies (Hall, 1981). Findley et al. (1975) suggested that this species is not restricted to vegetative zones. However, both *M. lucifugus* and *M. occultus* tend to occur near permanent sources of water (Findley et al., 1975; Harris, 1974).

These two taxa are similar in many respects but reportedly differ in others. Findley and Jones (1967) stated that montane and northern populations of *M. lucifugus* and *M. occultus* have darker membranes and a more richly colored pelage than lowland and

southern bats. We concur that adult *M. occultus* in New Mexico tend to have reddish pelage, whereas adult *M. lucifugus* in northern Colorado and Wyoming have brown pelage with burnished tips. Other morphological differences between these bats are: rostrum longer in *M. occultus* than *M. lucifugus* (Findley and Jones, 1967); slope of forehead from rostrum to top of braincase gradual in *M. occultus*, abrupt in *M. lucifugus* (Hoffmeister, 1986); area of rostrum greater, when compared to braincase, in *M. occultus*, less in *M. lucifugus* (Miller and Allen, 1928); second upper premolars often absent in *M. occultus*, present in *M. lucifugus* (Barbour and Davis, 1970); sagittal crest present in *M. occultus*, absent in *M. lucifugus* (Findley and Jones, 1967).

Above differences notwithstanding, the taxonomic status of *M. occultus* is unresolved. Hollister (1909) described *M. occultus* based on specimens from Needles, California. In the same paper, he named another bat (from the White Mountains near Ruidoso, New Mexico) as *Myotis baileyi*. Miller and Allen (1928) relegated *M. baileyi* to synonymy with *M. occultus* and recognized

M. occultus as a species separate from *M. lucifugus*. Based on cranial morphology and number of premolars, Findley and Jones (1967) concluded that *M. occultus* was a subspecies of *M. lucifugus*, as did Barbour and Davis (1970). In a phenetic analysis of the genus *Myotis*, Findley (1972:43–44) re-examined the taxonomic status of *M. occultus* and stated, “either *M. occultus* is a *lucifugus* that has converged toward the *grisescens* group phenome, or the field relationships of [*M. lucifugus*] *carissima* and *occultus* have not been fully elucidated.” Findley et al. (1975) subsequently listed *M. occultus* as a subspecies of *M. lucifugus*, as did Hall (1981). Hoffmeister (1986) analyzed a suite of cranial characters using principal-components and canonical-variates analyses and concluded that *M. lucifugus* and *M. occultus* were distinct species. Koopman (1993, 1994) listed *M. occultus* as a synonym of *M. lucifugus*. Our objective was to assess genetic relationships between these nominal taxa and thereby to resolve their uncertain taxonomic relationship.

MATERIALS AND METHODS

We performed protein electrophoresis of allozymes from 142 specimens of *Myotis* (Appendix I). Tissues (heart, liver, kidney, muscle, and embryos) were frozen in liquid nitrogen in the field and later transferred to the Division of Biological Materials Museum of Southwestern Biology, University of New Mexico. Voucher specimens are housed in the Sternberg Museum of Natural History at Fort Hays State University and the United States Geological Survey-Biological Survey Collection at the Museum of Southwestern Biology.

Of the 142 specimens used for electrophoretic analysis (Appendix I), 101 were collected in 1995. The remainder came from the Division of Biological Materials at the University of New Mexico. Tissues were grouped into nine samples referable (based primarily on color of pelage and geographic range) to *M. l. carissima* (samples 8 and 9; Appendix I), *M. occultus* (samples 3, 4, 5, 6, and 7; Appendix I), or intergrades of the two (samples 1 and 2; Appendix I).

Procedures used for horizontal starch-gel electrophoresis were modified from those of Selander

et al. (1971). Loci analyzed by Reduker et al. (1983) were used as a template for the analysis, but some modifications were made including use of alternate buffer systems (when needed), additional loci, and increased running time for gels. We examined the following loci and buffer systems: continuous tris-citrate I buffer system with the lactate dehydrogenase (LDH-1, 2; EC 1.1.1.27) and malate dehydrogenase (MDH-1, 2; EC 1.1.1.37) loci; continuous tris-citrate II buffer system with the α -glycerophosphate dehydrogenase (α -GPD; EC 1.1.1.8), malic enzyme (ME-1; EC 1.1.1.40), glutamate-oxaloacetate transaminase (GOT-1,2; EC 2.6.1.1), phosphoglucomutase (PGM-1; EC 2.7.5.1), 6-phosphogluconate dehydrogenase (6-PGD; EC 1.1.1.44), adenylate kinase (ADK-1,2; EC 2.7.4.3), creatine kinase (CK-1; EC 2.7.3.2), and superoxide dismutase (SOD-1,2; EC 1.15.1.1) loci; discontinuous tris-citrate buffer system with general protein (GP-1,2; non-enzymatic proteins) and peptidase (PEP-B,C,D; EC 3.4.11) loci.

Letters of the alphabet were used to represent alleles. The most common homozygote allele for each locus was designated as A, B represented a rarer fast allele, and C represented a rarer slow allele. Heterozygotes were viewed as combinations of two different homozygote alleles and were represented as medium-fast (A \times B) and medium-slow (A \times C).

Data were recorded and analyzed using BIOSYS-1 (Swofford and Selander, 1989). Chi-square and fixation-index values (F_i) were calculated and compared to the Hardy-Weinberg model for deviation in allelic frequencies. F_i -values are bounded by 1 and -1 and indicate the direction of deviation from the Hardy-Weinberg equilibrium—negative values for more heterozygotes than expected, positive values for fewer heterozygotes (Svoboda et al., 1985).

Three F -coefficients, commonly known as Wright's F -statistics, were calculated using BIOSYS-1. These coefficients show correlation and are not to be associated with F -statistics used in the analysis of variance (Hedrick, 1983). The three coefficients include F_{ST} , F_{IT} , and F_{IS} , subscripts representing genetic variability in the total population (T), subpopulations (S), and individuals (I—Hedrick, 1983). The F_{ST} -coefficient evaluates level of heterozygosity in subpopulations resulting from genetic drift (Hartl, 1981). F_{ST} is bounded by 0 and 1 (Hedrick, 1983); an F_{ST} -value of zero indicates that sub-

populations are identical with respect to frequency of alleles, whereas an F_{ST} -value of one means different alleles are fixed in different subpopulations (Svoboda et al., 1985). The F_{IS} -coefficient evaluates level heterozygosity in individuals resulting from non-random mating within a subpopulation (Hartl, 1981). Heterozygosity levels of individuals relative to the total population are represented by the F_{IT} -coefficient (Hartl, 1981). Both F_{IS} and F_{IT} show the amount of deviation from the Hardy-Weinberg model within subpopulations and total populations (Hedrick, 1983). An excess of heterozygotes is represented as a negative value for F_{IS} or F_{IT} , whereas a deficiency of heterozygotes is viewed as a positive value (Hedrick, 1983). A matrix composed of Rogers' genetic similarity index and Nei's unbiased genetic identity index was created using BIOSYS-1 (Swofford and Selander, 1989).

RESULTS

We obtained an average of 10 specimens/capture site in New Mexico (Appendix I). Habitats at these sites ranged from ponderosa pine to desert scrubland around intermittent creeks and stock ponds. In Colorado, we sampled bats from maternity colonies at two sites. The first colony was in Monte Vista in the San Luis Valley, near the hypothesized area of intergradation between *M. lucifugus* and *M. occultus* (Findley and Jones, 1967). The surrounding area consisted of cottonwoods, houses, and irrigation ditches. The other colony, located west of Trinidad, Colorado, occupied the attic of a guest house at the Bar-NI Ranch. Habitat included ponderosa pine forest with a pond and permanent stream nearby.

We obtained no specimens from central or northern Colorado but collected specimens from a colony in an unoccupied building near the Green River at Seedska-dee National Wildlife Refuge in southern Wyoming. Nearby habitat for those bats consisted of riparian areas, open grassland, and forests.

We also analyzed 29 specimens of *M. l. carissima* collected at the type locality, Yellowstone National Park, by A. Parkinson in

1983 and housed at the University of New Mexico Museum of Southwestern Biology. The surrounding habitat at Yellowstone National Park consisted primarily of ponderosa pine (*Pinus ponderosa*), Douglas fir (*Pseudotsuga taxifolia*), and a lake.

Of the 20 loci studied, nine were polymorphic (Table 1); lactate dehydrogenase (LDH-1,2), α -glycerophosphate dehydrogenase (α -GPD), malic enzyme (ME-1), glutamate-oxaloacetate transaminase (GOT-1), phosphoglucosmutase (PGM-1), 6-phosphogluconate dehydrogenase (6-PGD), and adenylate kinase (ADK-1,2). No fixed allelic differences were found between *M. lucifugus* and *M. occultus*.

The chi-square values revealed that deviations in allelic frequencies from Hardy-Weinberg equilibrium were significant for ME-1 in samples 2, 7, 8, and 9. Fixation indices for samples 2, 7, and 8 at the ME-1 locus displayed a significant deficiency of heterozygotes (Table 2). The fixation index for sample 5 at the LDH-1 locus indicated a significant excess of heterozygotes (Table 2).

Mean F_{IS} revealed that random mating occurred within samples (Table 3). F_{IS} and F_{IT} for ME-1 indicated a deficiency of heterozygotes; however, there is an excess of heterozygotes for the other polymorphic loci. Mean F_{IT} (0.101), a positive value, indicated that there was an overall deficiency of heterozygotes compared to the Hardy-Weinberg model. The small mean F_{ST} (0.081) indicated a low heterogeneity in allelic frequencies (Hedrick, 1983).

Coefficients for Nei's index ranged from 0.992 to 1.000 and coefficients for Rogers' index ranged from 0.968 to 0.997 (Table 4). Those values indicated that there was little genetic differentiation in our sample and suggested that gene flow was not restricted among the nine subpopulations.

DISCUSSION

Controversy over the taxonomic status of *M. occultus* has resulted from different interpretations of the significance of morpho-

TABLE 1.— Allelic frequencies of polymorphic loci (see Appendix I for location of samples). Samples 8 and 9 represent *Myotis lucifugus*, samples 3–7 represent *M. occultus*, and samples 1 and 2 represent intergrades of the two.

Locus	Samples								
	1	2	3	4	5	6	7	8	9
LDH-1 (n)	15	14	16	12	4	18	20	14	29
A	0.900	0.893	0.500	0.708	0.500	0.639	0.725	0.536	0.586
B	0.100	0.107	0.500	0.292	0.500	0.361	0.275	0.464	0.414
C									
LDH-2 (n)	15	14	16	12	4	18	20	14	29
A	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	0.948
B									
C									0.052
α -GPD (n)	15	14	16	12	4	18	20	14	28
A	1.000	0.964	1.000	1.000	1.000	0.944	1.000	0.929	0.893
B		0.036				0.056		0.071	0.107
C									
ME-1 (n)	15	14	16	12	4	18	20	13	29
A	1.000	0.929	1.000	1.000	0.875	1.000	0.950	0.923	0.862
B					0.125		0.050		0.052
C		0.071						0.077	0.086
GOT-1 (n)	15	14	16	12	4	18	20	14	29
A	1.000	1.000	0.969	1.000	1.000	1.000	1.000	1.000	1.000
B			0.031						
C									
PGM-1 (n)	15	14	16	12	4	18	20	14	29
A	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	0.966
B									0.034
C									
6-PGD (n)	15	14	16	12	4	18	20	14	29
A	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	0.983
B									
C									0.017
ADK-1 (n)	15	14	16	12	4	18	20	14	29
A	1.000	1.000	1.000	1.000	1.000	1.000	1.000	0.964	1.000
B									
C								0.036	
ADK-2 (n)	15	14	16	12	4	18	20	14	29
A	1.000	1.000	1.000	1.000	1.000	0.972	1.000	1.000	1.000
B									
C						0.028			

logical differentiation between these taxa. Previous genetic studies of *M. lucifugus* did not examine the relationship of *M. lucifugus* and *M. occultus*. For example, Baker and Patton (1967) concluded that karyotypes would not be useful for separating species within the genus *Myotis*, and Herd and Fen-

ton's (1983) electrophoretic study examined only the relationship between *M. yumanensis* and *M. lucifugus*.

We found *M. lucifugus* and *M. occultus* to be genetically similar. In fact, the high similarity values (> 0.968) suggest a high degree of interconnectedness resulting from

TABLE 2.—Chi-square values with corresponding fixation indices used in comparison of *Myotis lucifugus* and *M. occultus* (see Appendix 1 for location of samples).

Locus	Samples									
	1	2	3	4	5	6	7	8	9	
LDH-1	χ^2	0.120	8.320	0.017	1.699	3.000	0.055	0.450	5.157	0.417
	$F(i)$	-0.111	0.627	0.000	-0.412	-1.000	-0.084	0.122	0.569	-0.137
LDH-2	χ^2									0.057
	$F(i)$									-0.055
GOT-1	χ^2			0.000						
	$F(i)$			-0.032						
α -GPD	χ^2		0.000			0.030		0.040		0.331
	$F(i)$		-0.037			-0.059		-0.077		-0.120
ME-1	χ^2		27.040			0.000		39.030	25.040	40.210
	$F(i)$		1.000			-0.143		1.000	1.000	0.720
ADK-1	χ^2								0.000	
	$F(i)$								-0.037	
ADK-2	χ^2					0.000				
	$F(i)$					-0.029				
PGM-1	χ^2									0.018
	$F(i)$									-0.036
6-PGD	χ^2									0.000
	$F(i)$									-0.018

extensive gene flow between taxa (Patton, 1985). However, some authors have concluded that taxa in their analyses were specifically distinct regardless of high similarity values. For example, Reduker et al. (1983) concluded that *M. milleri* and *M. evotis* were distinct species despite a moderately high similarity value of 0.898 because they found a fixed allelic difference at the esterase-1 locus. Herd and Fenton (1983)

judged that *M. lucifugus* and *M. yumanensis* were specifically distinct with a mean similarity value of 0.700 because they found three fixed allelic differences. In our analysis, bats collected from southern New Mexico (which exhibited morphological features of *M. occultus*), Yellowstone, Wyoming (the type locality for *M. lucifugus carissima*), and Colorado (possible intergrades between the two) exhibited no fixed allelic differences.

TABLE 3.—Summary of F-statistics for polymorphic loci as calculated by BIOSYS-1 (Swoford and Selander, 1989) for the study of relationships between *Myotis lucifugus* and *M. occultus*.

Locus	F_{IS}	F_{IT}	F_{ST}
LDH-1	-0.095	0.009	0.095
LDH-2	-0.055	-0.006	0.046
α -GPD	-0.084	-0.031	0.049
ME-1	0.618	0.640	0.059
GOT-1	-0.032	-0.003	0.028
PGM-1	-0.036	-0.004	0.031
6-PGD	-0.018	-0.002	0.015
ADK-1	-0.037	-0.004	0.032
ADK-2	-0.029	-0.003	0.025
\bar{X}	0.022	0.101	0.081

The overall deficiency of heterozygotes of individuals within the total population (F_{IT}) and relatively low heterogeneity of allelic frequencies of samples within the total population (F_{ST}) suggest that these samples are not in Hardy-Weinberg equilibrium. Our data do not support strong inbreeding or the Wahlund effect, but additional samples from north of Wyoming and west of New Mexico may fully elucidate these relationships. The fact that most bats were collected from potentially isolated populations in montane regions may be responsible for the deviation from zero of the mean F_{IS} (0.022). Also, this deviation is small (near zero), suggesting that bats were from a natural

TABLE 4.—Matrix of Nei's unbiased genetic index (above diagonal) and Roger's genetic similarity index (below diagonal) for *Myotis lucifugus* (samples 8 and 9), *M. occultus* (samples 3–7), and intergrades of the two (samples 1 and 2).

Sam- ples	Location	Samples								
		1	2	3	4	5	6	7	8	9
1	Las Animas Co., Colorado		1.000	0.992	0.999	0.994	0.997	0.999	0.994	0.994
2	Rio Grande Co., Colorado	0.994		0.993	0.999	0.994	0.997	0.999	0.995	0.996
3	Catron Co., New Mexico	0.978	0.973		0.999	1.000	1.000	0.998	1.000	0.999
4	Cibola Co., New Mexico	0.990	0.985	0.988		1.000	1.000	1.000	0.999	0.999
5	Grant Co., New Mexico	0.974	0.973	0.992	0.983		1.000	1.000	1.000	1.000
6	Otero Co., New Mexico	0.983	0.981	0.987	0.992	0.983		1.000	1.000	1.000
7	Socorro Co., New Mexico	0.989	0.987	0.985	0.997	0.985	0.989		0.999	0.999
8	Sweetwater Co., Wyoming	0.973	0.978	0.987	0.982	0.987	0.987	0.982		1.000
9	Yellowstone, Park Co., Wyom- ming	0.968	0.973	0.978	0.977	0.981	0.982	0.978	0.986	

population that is within Hardy-Weinberg equilibrium (Hartl, 1981).

Our results support the conclusions of Findley and Jones (1967). There do not appear to be any obvious physical barriers that would prevent gene flow between *M. l. carissima* and *M. l. occultus*, despite obvious morphological differences between these taxa. Causes of morphological differentiation between *M. l. occultus* and *M. l. carissima* are not known, although Findley and Jones (1967) found that skull size in *M. lucifugus* was correlated with the number of other species of *Myotis* present at a site. We believe these cranial differences may reflect selection or availability of prey, but this needs to be examined further.

Harris (1974) postulated that, in the late Pleistocene, *M. l. occultus* (which typically inhabited highlands of the Southwest) may have occupied both intermediate (abandoned by *M. yumanensis* and *M. velifer*) and upper elevations. If *M. l. carissima* had invaded these highlands, there would have been too much interbreeding to maintain differences now observed between the two subspecies (Harris, 1974). In this scenario, *M. l. carissima* would have occurred north of New Mexico where interbreeding would have been enhanced by the broader zone of contact produced by a larger area of mesic conditions. Harris (1974) mentioned other possible explanations for differences be-

tween *M. l. occultus* and *M. l. carissima*, and we concur with him that they seem less plausible than the one given.

Morphology is known to be influenced by diverse environmental selective pressures, but genic differences often remain independent (Patton, 1984; Patton and Feder, 1978; Patton et al., 1979). Conservative attributes of genetic analysis support the conclusion that *M. occultus* and *M. lucifugus* are essentially identical. Genic data suggest that *M. occultus* could be synonymized with *M. lucifugus* were it not for the well-documented morphological differences between them. Therefore, we propose that the name *occultus* be retained as a subspecies of *M. lucifugus*.

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APPENDIX I

Specimens Used During Protein Electrophoretic Analysis

Intergrades between *M. l. carissima* and *M. l. occultus*—Sample 1. COLORADO ($n = 15$). Las Animas Co.: Bar-NI Ranch, 0.5 mile S Stonewall, 15. Sample 2. COLORADO ($n = 14$). Rio Grande Co.: Monte Vista, 14.

Myotis lucifugus occultus—Sample 3. NEW MEXICO ($n = 16$). Catron Co.: Gila National Forest, at junction of Forest Service Road 119 and Forest Service Road 159 (by road), Quaking Aspen Creek, 1; Gila National Forest, Bear-wallow Tank, 1; Gila National Forest, Sheep Springs, 3; Gila National Forest, 6 miles E Bear Wallow Lookout Tower, 9; Gila National Forest, 24 mi S (by road) Reserve, Forest Service Road 626, Devils Park 2. Sample 4. NEW MEXICO ($n = 12$). Cibola Co.: Cibola National Forest, Agua Fria Creek, 2; Cibola National Forest, Forest Service Road 504, pond (by road), 1; Cibola National Forest, 1 mile W Ojo Rodondo campground, pond (by road), 9. Sam-

ple 5. NEW MEXICO ($n = 4$). Grant Co.: Gila National Forest, Meadow Creek, 4. Sample 6. NEW MEXICO ($n = 18$). Lincoln Co.: Cedar Creek, 1. Otero Co.: Lincoln National Forest, Cloudcroft District, Sacramento Lake, 1; Lincoln National Forest, Sixteen Springs Canyon, stock pond (by road), 1; Lincoln National Forest, Lightning Lake, 1; Lincoln National Forest, Forest Service Road 607A, well tank (by road), 14. Sample 7. NEW MEXICO ($n = 20$). Socorro Co.: Bosque Del Apache Headquarters, 2; Bosque Del Apache Headquarters, equipment

barn, 10; Bosque Del Apache, 2; Bosque Del Apache Wildlife Refuge, 3.6 miles N Headquarters (by road), 2; Bosque Del Apache Wildlife Refuge, 1 mile N Headquarters (between units 18A, 17B, and 27), 2; Bosque Del Apache Wildlife Refuge, 3.4 miles N, 1.1 mile E of Headquarters (between units 5, 6, and 9), 2.

Myotis lucifugus carissima—Sample 8. WYOMING ($n = 14$). Sweetwater Co., Seedskaadee National Wildlife Refuge, Headquarters, Blockhouse, 14. Sample 9. WYOMING ($n = 29$). Yellowstone National Park, Lake Hotel, 29.