

On the taxonomy of *Myotis lucifugus*

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BACKGROUND SUMMARY

Morales & Carstens (2018) undertook a genetic analysis, based on Ultra-Conserved Elements (UCE) of specimens of each of the 5 currently recognized subspecies of *Myotis lucifugus* (Le Conte, 1831) in North America (*lucifugus* (Le Conte, 1831), *alascensis* Miller, 1897, *carissima* Thomas, 1904, *pernox* Hollister, 1911, and *relictus* Harris, 1974), together with specimens of *Myotis evotis*, *M. keenii*, *M. occultus*, *M. sodalis*, *M. thysanodes*, and *M. volans*. Using a statistical analysis method that takes into account the possibility of some degree of introgression among taxa, they concluded that the subspecies of *Myotis lucifugus* may not be each other's closest relatives, and should potentially be considered as distinct species. As a result, the American Society of Mammalogists' Mammal Diversity Database version 1.5 (published 11 June 2021) recognized each of the former subspecies as full species. However, the batnames.org database (Version 2022B) has continued to treat them together as one species.

Given the current listing of the species *Myotis lucifugus* as Endangered in Canada under the Species at Risk Act, and the proposed listing of this species as Endangered under the U.S. Endangered Species Act, the classification of the species is of more than academic interest—it also has potential implications for the legal conservation status of these bats. As a result, the Global Bat Taxonomy Working Group was asked to review the situation and make a recommendation on an appropriate treatment for the subspecies of *Myotis lucifugus*.

RECOMMENDATION

We recommend that *M. l. alascensis*, *M. l. carissima*, *M. l. pernox*, and *M. l. relictus* should continue to be recognized as subspecies of *Myotis lucifugus*, at least until such time as more conclusive information is provided supporting their elevation to species status. This recommendation is based on the following considerations.

Given the long-standing taxonomic status of this group as a single species, as well as the legal status of the species, a high standard of evidence should be required before concluding that it is, in fact, a species complex. This evidence should include a combination of robust genetic and morphological analyses from throughout the range of each taxon.

While Morales & Carstens (2018) provide some evidence for genetic differentiation among populations of *Myotis lucifugus*, they presented no accompanying analyses of morphological or other characters used to differentiate these populations. Importantly, it is unclear how they actually identified the different subspecies. Their paper states (p.758): “All specimens included in this study were carefully identified in the field first and subsequently confirmed by curators of museum collections” citing the supplementary material as a reference. However, no information was provided in the supplementary material on any morphological or other characters used to differentiate subspecies of *Myotis lucifugus* (or any other species), nor on the names of the field researchers or curators who identified them. Furthermore, in many cases, the museum collection and catalog number of voucher specimens are lacking from the supplementary material, particularly for the specimens from which Tanya Dewey provided DNA extractions, and for many specimens even the sex was not reported. Thus, it is unclear whether subspecies were determined based on any criteria other than geographic range or a potentially subjective opinion of the collector and/or curator.

Despite the lack of morphological analyses, Morales & Carstens (2018) based their genetic models on the assumption that each subspecies represents a taxonomically uniform entity. No tests were presented to show that all individuals within a subspecies are actually more similar to each other than they are to individuals from other populations. For example, no data were presented to show whether the 4 specimens assigned to *M. l. lucifugus* from South Dakota are more similar to specimens from eastern North America than they are to the geographically close specimen assigned to *M. l. carissima* from Nebraska. Thus, it is unclear whether these subspecies actually represent distinct entities that can be distinguished from each other based on either morphological or genetic characters.

While the Morales & Carstens (2018) data set included moderate geographic sampling for some taxa, large portions of the traditionally recognized range of several subspecies were not sampled, and two taxa, *relictus* and *pernox*, were sampled based on only 2 and 1 specimens respectively (Morales & Carstens 2018; Table 1). Of particular concern, Morales & Carstens (2018) provide a map showing *M. l. lucifugus* occurring as far west as Alaska, but no specimens from anywhere in Canada or Alaska were analyzed by Morales & Carstens (2018). Thus, even if there might be more than one species in what is currently called *M. lucifugus*, it is unclear where the species boundaries should be, and whether any of these taxa are sympatric or whether they are all allopatric.

Finally, the authors themselves suggest the possibility that gene flow between nonsister lineages could “lead to the apparent paraphyly and unclear lineage relationships of the *M. lucifugus* subspecies.” Their data show that geographic proximity is a predictor of apparent phylogenetic relationships, and they note that it is not possible with the available data to determine whether this represents historic or ongoing gene flow. Thus, it is quite possible that the various populations of *Myotis lucifugus* periodically hybridize with other species of *Myotis* within their range, leading to introgression. The authors even note, in their discussion, that further development of analytic methods is needed to understand phylogenetic relationships. As

such, their conclusion that these taxa are paraphyletic and should be elevated to species level seems premature, given the cautions they, themselves present. Based on data from Europe, Nicole Foley (unpublished abstract presented at 19th International Bat Research Conference, 8 August 2022) suggested that, due to high levels of introgression, the phylogenetic signal in at least some species of *Myotis* may be limited to less than 57% of the genome, primarily near chromosome centers. If a similar pattern applies to North American *Myotis*, this would imply that resolving relationships would require mapping variation onto chromosomes.

Thus, in conclusion, while Morales & Carstens (2018) suggest the intriguing possibility that *Myotis lucifugus* may represent a species complex, we argue that the evidence is not sufficient to warrant any changes in the taxonomic status without substantial additional genetic and morphological data from throughout the range of each form, including detailed documentation of how specimens have been identified as belonging to particular subspecies. We also note that examination of the type specimens of each subspecies would be essential to determine which may be the most appropriate names if there are multiple species.

In terms of next steps, we note that two other recently published genetic studies of *Myotis lucifugus* had quite extensive geographic coverage of the species (Vonhof et al. 2015; Wilder et al. 2015) and combined analyses of data from all of these studies may lead to further insights, though none of them include morphological analyses. We also note that we did not consider the taxonomic status of *Myotis occultus* Hollister, 1909 from New Mexico and Arizona, which some authors consider a subspecies of *Myotis lucifugus*, and which Morales & Carstens (2018) show is genetically most similar to *M. l. carissima* and *M. l. relictus*. A comprehensive analysis of the taxonomy of this group should consider all of these forms.

REFERENCES

- Mammal Diversity Database. (2022). Mammal Diversity Database (Version 1.9) [Data set]. Zenodo. <http://doi.org/10.5281/zenodo.4139818>
- Morales, Ariadna E; Carstens, Bryan C (2018), Evidence that *Myotis lucifugus* 'subspecies' are five nonsister species, despite gene flow. Syst. Biol. 67(5):756–769. DOI: 10.1111/csp2.12805
- Morales, Ariadna E; Carstens, Bryan C (2018), Data from: Evidence that *Myotis lucifugus* 'subspecies' are five nonsister species, despite gene flow, Dryad, Dataset, <https://doi.org/10.5061/dryad.9d6b2>
- Simmons, N.B. and A.L. Cirranello. 2022. Bat Species of the World: A taxonomic and geographic database. Version 2022B. <https://batnames.org>
- Wilder, AP; Kunz, TH; Sorenson, MD. 2015. Population genetic structure of a common host predicts the spread of white-nose syndrome, an emerging infections disease in bats. Molecular ecology 24: 5495-5506. <https://onlinelibrary.wiley.com/share/A6K5W9WMCF2JXB5EHHJ3?target=10.1111/mec.13396>
- Vonhof, MJ; Russell, AL; Miller-Butterworth, CM. 2015. Range-Wide Genetic Analysis of Little Brown Bat (*Myotis lucifugus*) Populations: Estimating the Risk of Spread of White-Nose Syndrome. PLoS ONE 10(7): e0128713. <https://doi.org/10.1371/journal.pone.0128713>