

Mating Behavior as a Possible Cause of Bat Fatalities at Wind Turbines

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ABSTRACT Bats are killed by wind turbines in North America and Europe in large numbers, yet a satisfactory explanation for this phenomenon remains elusive. Most bat fatalities at turbines thus far occur during late summer and autumn and involve species that roost in trees. In this commentary I draw on existing literature to illustrate how previous behavioral observations of the affected species might help explain these fatalities. I hypothesize that tree bats collide with turbines while engaging in mating behaviors that center on the tallest trees in a landscape, and that such behaviors stem from 2 different mating systems (resource defense polygyny and lekking). Bats use vision to move across landscapes and might react to the visual stimulus of turbines as they do to tall trees. This scenario has serious conservation and management implications. If mating bats are drawn to turbines, wind energy facilities may act as population sinks and risk may be hard to assess before turbines are built. Researchers could observe bat behavior and experimentally manipulate trees, turbines, or other tall structures to test the hypothesis that tree bats mate at the tallest trees. If this hypothesis is supported, management actions aimed at decreasing the attractiveness of turbines to tree bats may help alleviate the problem. (JOURNAL OF WILDLIFE MANAGEMENT 72(3):845–849; 2008)

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Bats are killed at wind power facilities all over the world, with estimates of current fatalities ranging as high as 70 bats killed per turbine per year and future projections ranging into the tens of thousands per year at a continental scale (Kunz et al. 2007, Arnett et al. 2008). Bat fatalities are increasing, apparently with the deployment of larger turbines, and the mystery of why bats are so vulnerable to such structures remains unsolved (Barclay et al. 2007). Is it a simple case of flying in the wrong place at the wrong time? Are bats attracted to turbines? Why are some species more affected than others? Researchers have proposed several hypotheses for explaining the causes of bat fatalities at wind turbines, yet none currently stand out as being most likely nor have they been tested (reviewed by Kunz et al. 2007).

Cryan and Brown (2007) postulated that fatalities of bats at wind turbines may be a consequence of flocking and mating activities. In particular, Cryan and Brown (2007) presented evidence suggesting that species of *Lasiurus* in North America not only aggregate during autumn migration but actively mate during this time as well. Herein I present additional evidence for autumn aggregation and mating, and outline how fatalities at turbines may be related to the reproductive strategies of bats that evolved to roost in trees. In particular, I hypothesize that bat fatalities at wind turbines result from mating behaviors that center around the tallest trees in the landscape and that this phenomenon may involve 2 different mating systems: resource defense polygyny and lekking.

Patterns of fatalities offer potential clues as to why bats collide with wind turbines. The first clear pattern concerns similar behaviors of the species involved. Thus far, most bats killed at turbines roost in trees or foliage during much of the year (hereafter, tree bats) and migrate across several degrees of latitude. Tree bats killed by turbines in North America include the hoary bat (*Lasiurus cinereus*), eastern red bat (*L.*

borealis), and silver-haired bat (*Lasionycteris noctivagans*; Johnson 2005, Kunz et al. 2007, Arnett et al. 2008). Researchers have reported similar fatality patterns of bats at turbines in Europe, where species most widely affected are the noctule bat (*Nyctalus noctula*), Leisler's bat (*N. leisleri*), Nathusius' pipistrelle (*Pipistrellus nathusii*), common pipistrelle (*P. pipistrellus*), soprano pipistrelle (*P. pygmaeus*), and parti-colored bat (*Vespertilio murinus*; EUROBATS 2005, Brinkmann et al. 2006a, b). These European species also rely on trees (and buildings) as roosts during much of the year (Schober and Grimmberger 1989, Greenway and Hutson 1990, Jenkins et al. 1998, Boonman 2000, Jaberg and Blant 2003) and make latitudinal migrations (Baker 1978, Hutterer et al. 2005, Ahlen et al. 2007). Furthermore, peaks in fatalities at wind turbines in both North America and Europe predominantly occur during late summer and autumn (EUROBATS 2005, Johnson 2005, Brinkmann et al. 2006a, Cryan and Brown 2007, Kunz et al. 2007). Consistent fatality patterns among tree-roosting bats on different continents indicate that they share common behaviors during this late-summer and autumn period that place them at risk of collision with wind turbines.

There are several reasons why tree bats may have evolved mating behaviors that focus on the tallest trees in the landscape. Bats rely on vision for long-distance navigation and silhouettes of the tallest trees are simple visual cues that bats could orient toward from a distance greater than the distance from which they could detect acoustic cues (Griffin 1970). Taller trees also potentially provide more roosting opportunities for bats. Studies reveal a positive relationship between height of trees and probability of use by both foliage- and cavity-roosting bats (Kalcounis-Rüppell et al. 2005). The tallest trees are typically among the most mature in a forest and as trees age they are more likely to have cavities, loose bark, crevices, and suitable foliage in which bats can roost. Selection should favor behaviors that increase the chances of bats finding suitable roosts and tree height is

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a plausible proxy for suitability, particularly for tree bats traveling through or over unfamiliar areas during migration. Selection should also favor behaviors that increase the probability of bats efficiently finding mates. In most of the bat species killed by turbines in both North America and Europe, the sexes tend to differ in geographic distribution during spring and early summer (Strelkov 1969, Baker 1978, Cryan 2003). Sex differences tend to disappear during late summer and autumn, when most mating activity is observed. I suggest that tree bats use the highest trees in a landscape as rendezvous points during the mating period and that this behavior places them at risk of collision with the blades of wind turbines. Reproductive bats may be attracted to turbines when looking for mating opportunities, mistaking turbines for the tallest trees. Such a scenario seems plausible in species of tree bats in which sexes are segregated across large forested areas until late summer, when they must come together to mate while migrating through potentially unfamiliar landscapes.

Bats exhibit a diversity of mating systems, yet the specifics of mating have only been characterized for a small proportion of bat species (approx. 7%; McCracken and Wilkinson 2000). The most complete information on behavior and mating systems of bat species killed by wind turbines comes from Europe. Species of tree bats found dead most frequently at turbines in Europe (*N. leisleri*, *N. noctula*, *P. nathusii*, *P. pipistrellus*, *P. pygmaeus*, and *V. murinus*) stand out from the European bat fauna in that males establish and defend mating territories around roost sites during late summer and autumn (Gerell and Lundberg 1985, Kronwiter 1988, Zagmajster 2003, Sachtelenben and von Helversen 2006). During peak mating periods, males of these species are known to engage in songflight, vocalizations that presumably advertise their territories to receptive females and competitors (von Helversen and von Helversen 1994, Barlow and Jones 1997, Pfalzer and Kusch 2003, Zagmajster 2003). Such observations indicate resource defense polygyny, a common mating strategy employed by male bats when a resource needed by females is defensible (Altringham 1996, McCracken and Wilkinson 2000). In the case of European tree bats, the resource being defended often is a roosting structure such as a tree cavity, bat box, or building. However, most observations of songflight and territorial defense by European tree bats were made at sites within a few meters of the ground and, thus, observable by researchers. It is likely that similar behaviors occur at less-observable heights of trees, especially heights opportunistically exploited by wide-ranging, latitudinal migrants. Considering the opportunistic nature of bats and the potential for local environmental conditions to influence intraspecific variation in roost use, migration, and mating systems, observations of tree-roosting bats at nontree roosts may not represent the full range of behaviors that exist in nature (Fleming and Eby 2003, Kunz and Lumsden 2003, Wilkinson and McCracken 2003).

Migration decreases the chances that bats will form year-round groups with stable associations between sexes and

most species of migratory bats investigated thus far show highly polygynous and sometimes promiscuous mating systems (Fleming and Eby 2003). As discussed above, males of several bat species that roost in tree cavities tend to defend those sites during the mating period and exhibit resource defense polygyny. However, males of species that roost in abundant, ephemeral roosts like tree foliage may not be able to defend such sites when used by migratory females. Species of *Lasiurus* differ in roosting habits and behavior from European species, and most other Holarctic bats, because they roost alone or in small family groups (≤ 5) in tree foliage during spring and early summer (Barbour and Davis 1969). Foliage roosts used by female lasiurines during autumn migration are probably abundant and not easily defensible by males. Unless males could somehow anticipate and defend such roosts, mating success likely correlates with areas where the density of females is high during autumn migration (e.g., mountain ridges, passes, and coastlines) and selection would favor males that cluster at mating sites in those areas (i.e., hotspots; Bradbury et al. 1986). In areas of high bat density during migration, the tallest trees could serve as landscape features that help guide both males and females to mating arenas. Lekking is considered the default mating system for species in which females range widely or resources (food or roosts) are too finely distributed for males to defend, and the evolution of such behavior seems plausible in light of the potential importance of tall trees discussed above (Bradbury and Vehrencamp 1977, Bradbury 1981).

Species of *Lasiurus* (*L. borealis* and *L. cinereus*) are recovered in greater numbers and more frequently than other species of bats killed by wind turbines in North America (Arnett et al. 2008). Although lasiurines tend to live solitary lives throughout the summer, people have seen dense aggregations (i.e., flocks) of both *L. borealis* and *L. cinereus* during late summer and autumn (reviewed by Cryan and Brown 2007). Could these seasonal aggregations be associated with leks? Lekking is rare in mammals but Bradbury (1977) clearly documented it in a tropical frugivorous species of bat (*Hypsignathus monstrosus*; Höglund and Alatalo 1995). Common characteristics of lekking species include no paternal investment beyond mating, male aggregation and display at specific sites visited by females for mating, and that the only resources females obtain on the lek are gametes (Bradbury 1981, Höglund and Alatalo 1995). Scattered natural history observations from the past 2 centuries suggest that such characteristics exist in species of *Lasiurus*. Several authors reported concentrated groups of *L. cinereus* and *L. borealis* during late summer and autumn that were apparently segregated by sex, age, or both (Merriam 1884, Mearns 1898, Mumford 1973, Tumilson et al. 2002). Sex- and age-segregated flocks during mating periods are indicative of species that lek, and available evidence suggests that juvenile *L. cinereus* mature sexually during their first summer (Druecker 1972). In many reports, aggregations of *L. borealis* during late summer and autumn are predominantly composed of males (Myers 1960, Barbour and Davis

1969, Saugey et al. 1989, Tumblison et al. 2002). Intriguingly, fatalities of lasiurines at turbines are also skewed toward adult males, even in regions where adult males are not known to be abundant during spring and early summer (e.g., *M. L. cinereus* in the Appalachian Region; Findley and Jones 1964, Cryan 2003, Arnett et al. 2008). These seasonal aggregations of male bats, which otherwise live solitary lives, are suggestive of lek mating systems.

Other curious observations that indicate lekking are those that involve aggression between male *L. cinereus* gathered in large aggregations. For example, 200–300 *L. cinereus* were observed swarming “in daylight” around cottonwood trees in west-central Nevada on 28 August 1932 and 2 that fell to the ground fighting were males (Hall 1946:156). The eminent naturalist C. Hart Merriam (1884:179) wrote the following about his observations of *L. cinereus* in the Adirondack Mountains of northeastern New York:

“That the species ruts about the first of August there can be no reasonable doubt, for I saw more of them from the 30th of July till the 6th of August than I have seen in all before and since, and twelve adult specimens killed during that brief period were all males. They were not feeding, but were rushing wildly about, evidently in search of females. Many flew so high as to be entirely out of range though directly overhead”.

Bat lekking around turbines would likely include aerial courtship displays. As reviewed by Cryan and Brown (2007), almost every observation of mating in *L. borealis* ($n = 15$) involved bats that initiated copulation in mid-air. Aerial copulation has not been observed in other bat species, with the possible exception of *L. cinereus*, and may be the result of a mating system in which the sexes identify and assess each other in flight (C. Ramotnik, United States Geological Survey, personal communication; B. Thoman, Chattahoochee River Rod Company, personal communication). Sexual dimorphism is a common characteristic of lekking birds and bats and lasiurines are among the most sexually dimorphic bat species in North America (Allen 1939, Bradbury 1977, Williams and Findley 1979, Timm 1989, Oakes 1992). Although there are other selective forces influencing differences in body size and coloration between sexes of vertebrate species, such differences may help lasiurines discriminate the sex of conspecifics while flying (Ralls 1976, Myers 1978, Badyaev and Hill 2003). Curiously, many observations of aerial copulation by the sexually dichromatic *L. borealis* were made during twilight (Allen 1869, Murphy and Nichols 1913, Dearborn 1946, Stuewer 1948, Barbour and Davis 1969) and historical accounts describe high numbers of this species “flying about at all times of day” during autumn (E. A. Mearns, field journal entry from 1 November 1876, Smithsonian Institution, Washington, D.C.). The striking wing markings of lasiurines may serve as visual cues to conspecifics during flight and play a role in crepuscular or nocturnal mating displays. Aerial courtship display by species of *Lasiurus* around turbines is a possible factor

influencing their prevalence in fatality events in North America.

Management Implications

The possibility that bats are visually attracted to wind turbines, regardless of the mechanism, presents considerable management challenges. How can we preassess use of potential wind energy sites by bats if they are not present at a site before turbines are built and attract them? If bats visually orient toward turbines, will echolocation monitoring detect their presence? Because of these uncertainties, research into hypotheses of attraction should be prioritized. The hypothesis of general visual attraction to the tallest trees in a landscape could be tested through experimental manipulation of visibility or height of trees, turbines, or other suitable landscape structures. Similarly, increased bat activity during late summer and autumn should be observable at existing structures, such as municipal water towers and tall buildings, in areas where bats concentrate during migration. If bats are visually attracted to turbines, management measures, such as paint that is less visible to bats, could help minimize fatalities. The hypothesis of mating at wind turbines could be tested by the detection of distinct social calls often associated with mating (e.g., Pfalzer and Kusch 2003), the presence of sperm in the urethra and uteri of fatalities, or visual observations of bat mating (e.g., aerial coupling) at deactivated turbines. Aerial mating may be observable during twilight hours and researchers could conduct hourly fatality searches to determine the time of night that fatalities are most likely to occur. Natural behaviors exhibited by tree bats around tall landscape structures, especially behaviors that involve the gradual aggregation of individuals into leks, may be easier to observe at turbines with blades that are not rotating.

Although evidence is limited that tree bats in North America and Europe center their mating activities on the tallest trees in the landscape, the conservation implications of such a scenario are grave. If courtship and mating behavior occurs at turbines, then turbines not only have the potential to create population sinks that attract bats from far away, but also selectively kill those bats that are primed for reproduction. It is unknown how long such losses could be sustained by the affected species or if populations of current conservation concern (e.g., the endangered Hawaiian hoary bat [*L. cinereus semotus*]) are being impacted. In general, it is believed that migratory bat species, like those killed at wind turbines, thus far are more susceptible to population decline than are sedentary bats (Fleming and Eby 2003). Tree bats are the last mammalian species to regularly make unobstructed migratory movements that span entire continents. Loss of these bat species would equate to loss of an entire mammalian phenomenon.

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LITERATURE CITED

- Ahlen, I., L. Bach, H. J. Baagøe, and J. Pettersson. 2007. Bats and offshore wind turbines studied in southern Scandinavia. Swedish Environmental Protection Agency, Report 5571. <<http://www.naturvardsverket.se>>. Accessed 15 Aug 2007.
- Allen, G. M. 1939. Bats. Dover, New York, New York, USA.
- Allen, J. A. 1869. Catalogue of the mammals of Massachusetts: with a critical revision of the species. Bulletin of the Museum of Comparative Zoology 8:143–252.
- Altringham, J. D. 1996. Bats: biology and behavior. Oxford University Press, Oxford, United Kingdom.
- Arnett, E. B., W. K. Brown, W. P. Erickson, J. K. Fiedler, B. L. Hamilton, T. H. Henry, A. Jain, G. D. Johnson, J. Kerns, R. R. Koford, C. P. Nicholson, T. J. O'Connell, M. D. Piorkowski, and R. D. Tankersley. 2008. Patterns of bat fatalities at wind energy facilities in North America. Journal of Wildlife Management 72:61–78.
- Badyaev, A. V., and G. E. Hill. 2003. Avian sexual dichromatism in relation to phylogeny and ecology. Annual Review of Ecology, Evolution, and Systematics 34:27–49.
- Baker, R. R. 1978. The evolutionary ecology of animal migration. Holmes and Meier, New York, New York, USA.
- Barbour, R. W., and W. H. Davis. 1969. Bats of America. University Press of Kentucky, Lexington, USA.
- Barclay, R. M. R., E. F. Baerwald, and J. C. Gruver. 2007. Variation in bat and bird fatalities at wind energy facilities: assessing the effects of rotor size and tower height. Canadian Journal of Zoology 85:381–387.
- Barlow, K. E., and G. Jones. 1997. Differences in songflight calls and social calls between two phonic types of the vespertilionid bat *Pipistrellus pipistrellus*. Journal of Zoology, London 241:315–324.
- Boonman, M. 2000. Roost selection by noctules (*Nyctalus noctula*) and Daubenton's bats (*Myotis daubentonii*). Journal of Zoology 251:385–389.
- Bradbury, J. W. 1977. Lek mating behavior in the hammer-headed bat. Zeitschrift für Tierpsychologie 45:225–255.
- Bradbury, J. W. 1981. The evolution of leks. Pages 138–169 in R. D. Alexander and D. Tinkle, editors. Natural selection and social behavior: research and new theory. Chiron Press, New York, New York, USA.
- Bradbury, J. W., R. Gibson, and I. M. Tsai. 1986. Hotspots and the dispersion of leks. Animal Behavior 34:1694–1709.
- Bradbury, J. W., and S. L. Vehrencamp. 1977. Social organization and foraging of emballonurid bats. IV. Parental investment patterns. Behavioral Ecology and Sociobiology 2:19–29.
- Brinkmann, R., K. Mayer, F. Kretzchmar, and J. von Witzleben. 2006a. Auswirkungen von windkraftanlagen auf fledermäuse: ergebnisse aus dem Regierungsbezirk Freiburg mit einer handlungsempfehlung für die praxis. Publication of the German state of Baden-Württemberg, Regierungspräsidentium Freiburg, Germany. <www.rp.baden-wuerttemberg.de/servlet/PB/show/1196025/rpf-ref56-windkraft.pdf>. Accessed 15 Aug 2007. [In German.]
- Brinkmann, R., H. Schauer-Weissshahn, and F. Bontadina. 2006b. Survey of possible operational impacts on bats by wind facilities in southern Germany. Report to Administrative District of Freiburg—Department 56, Conservation and Landscape Management, Freiburg, Germany. <www.buero-brinkmann.de/downloads/Brinkmann_Schauer-Weissshahn_2006.pdf>. Accessed 15 Aug 2007.
- Cryan, P. M. 2003. Seasonal distribution of migratory tree bats (*Lasiurus* and *Lasionycteris*) in North America. Journal of Mammalogy 84:579–593.
- Cryan, P. M., and A. C. Brown. 2007. Migration of bats past a remote island offers clues toward the problem of bat fatalities at wind turbines. Biological Conservation 139:1–11.
- Dearborn, N. 1946. Miscellaneous notes. Journal of Mammalogy 27:178.
- Druceker, J. D. 1972. Aspects of reproduction in *Myotis volans*, *Lasionycteris noctivagans*, and *Lasiurus cinereus*. Dissertation, University of New Mexico, Albuquerque, USA.
- EUROBATS. 2005. Report of the Intersessional Working Group on Wind Turbines and Bat Populations. Tenth meeting of the EUROBATS Advisory Committee (Doc.EUROBATS.AC10.9), 25–27 April 2005, Bratislava, Slovak Republic. <http://www.eurobats.org/documents/pdf/AC10/Doc_AC10_9_Report_IWG_WindTurbines.pdf>. Accessed 15 May 2007.
- Findley, J. S., and C. Jones. 1964. Seasonal distribution of the hoary bat. Journal of Mammalogy 45:461–470.
- Fleming, T. H., and P. Eby. 2003. Ecology of bat migration. Pages 156–208 in T. H. Kunz and M. B. Fenton, editors. Bat ecology. The University of Chicago Press, Chicago, Illinois, USA.
- Gerell, R., and K. Lundberg. 1985. Social organization in the bat *Pipistrellus pipistrellus*. Behavioral Ecology and Sociobiology 16:177–184.
- Greenaway, F., and A. M. Hutson. 1990. A field guide to British bats. Bruce Coleman, Somerset, United Kingdom.
- Griffin, D. R. 1970. Migration and homing of bats. Pages 233–264 in W. A. Wimsatt, editor. Biology of bats. Volume II. Academic Press, New York, New York, USA.
- Hall, E. R. 1946. Mammals of Nevada. University of California Press, Berkeley, USA.
- Höglund, J., and R. V. Alatalo. 1995. Leks. Princeton University Press, Princeton, New Jersey, USA.
- Hutterer, R., T. Ivanova, C. Meyer-Cords, and L. Rodrigues. 2005. Bat migrations in Europe: a review of banding data and literature. Germany Agency for Nature Conservation, Bonn, Germany.
- Jaberg, C., and J. D. Blant. 2003. Spatio-temporal utilisation of roosts by the parti-colored bat *Vespertilio murinus* L., 1758 in Switzerland. Mammalian Biology 68:341–350.
- Jenkins, E. V., T. Laine, S. E. Morgan, K. R. Cole, and J. R. Speakman. 1998. Roost selection in the pipistrelle bat, *Pipistrellus pipistrellus* (Chiroptera: Vespertilionidae), in northeast Scotland. Animal Behaviour 56:909–917.
- Johnson, G. D. 2005. A review of bat mortality at wind-energy developments in the United States. Bat Research News 46:45–49.
- Kalcounis-Rüppell, M. C., J. Psyllakis, and R. M. Brigham. 2005. Tree roost selection by bats: an empirical synthesis using meta-analysis. Wildlife Society Bulletin 33:1123–1132.
- Kronwiter, F. 1988. Population structure, habitat use and activity patterns of the noctule bat, *Nyctalus noctula* Schreb., 1774 (Chiroptera: Vespertilionidae) revealed by radio-tracking. Myotis 26:23–85.
- Kunz, T. H., E. B. Arnett, W. P. Erickson, A. R. Hoar, G. D. Johnson, R. P. Larkin, M. D. Strickland, R. W. Thresher, and M. D. Tuttle. 2007. Ecological impacts of wind energy development on bats: questions, research needs, and hypotheses. Frontiers in Ecology and the Environment 5:315–324.
- Kunz, T. H., and L. F. Lumsden. 2003. Ecology of cavity and foliage roosting bats. Pages 3–89 in T. H. Kunz and M. B. Fenton, editors. Bat ecology. University of Chicago Press, Chicago, Illinois, USA.
- McCracken, G. F., and G. S. Wilkinson. 2000. Bat mating systems. Pages 321–362 in E. G. Crichton and P. H. Krutzsch, editors. Reproductive biology of bats. Academic Press, New York, New York, USA.
- Mearns, E. A. 1898. A study of the vertebrate fauna of the Hudson Highlands, with observations on the Mollusca, Crustacea, Lepidoptera, and the flora of the region. Bulletin of the American Museum of Natural History 10:303–352.
- Merriam, C. H. 1884. The mammals of the Adirondack Region, northeastern New York. Privately Published, New York, New York, USA.
- Mumford, R. E. 1973. Natural history of the red bat (*Lasiurus borealis*) in Indiana. Periodicum Biologorum 75:155–158.
- Murphy, R. C., and J. T. Nichols. 1913. Long Island fauna and flora—I. The bats (Order Chiroptera). Science Bulletin of the Museum, Brooklyn Institute of Arts and Sciences 2:1–15.
- Myers, R. F. 1960. *Lasiurus* from Missouri caves. Journal of Mammalogy 41:114–117.
- Myers, P. 1978. Sexual dimorphism in size in vespertilionid bats. The American Naturalist 112:701–711.
- Oakes, E. J. 1992. Lekking and the evolution of sexual dimorphism in birds: comparative approaches. American Naturalist 140:665–684.
- Pfalzer, G., and J. Kusch. 2003. Structure and variability of bat social calls: implications for specificity and individual recognition. Journal of Zoology 261:21–33.

- Ralls, K. 1976. Mammals in which females are larger than males. *The Quarterly Review of Biology* 51:245–276.
- Sachteleben, J., and O. von Helversen. 2006. Songflight behavior and mating system of the pipistrelle bat (*Pipistrellus pipistrellus*) in an urban habitat. *Acta Chiropterologica* 8:391–401.
- Saughey, D. A., D. R. Heath, and G. A. Heidt. 1989. The bats of the Ouachita Mountains. *Proceedings of the Arkansas Academy of Science* 43:71–77.
- Schober, W., and E. Grimmberger. 1989. *A guide to bats of Britain and Europe*. Hamlyn Group, London, United Kingdom.
- Strelkov, P. P. 1969. Migratory and stationary bats (Chiroptera) of the European part of the Soviet Union. *Acta Zoologica Cracoviensia* 14:393–436.
- Stuewer, F. W. 1948. A record of red bats mating. *Journal of Mammalogy* 29:180–181.
- Timm, R. M. 1989. Migration and molt patterns of red bats, *Lasiurus borealis* (Chiroptera: Vespertilionidae) in Illinois. *Bulletin of the Chicago Academy of Sciences* 14:1–7.
- Tumlison, R., T. Fulmer, T. Finley, and D. Saughey. 2002. Bats of the Jessieville Ranger District, Ouachita National Forest, Arkansas. *Journal of the Arkansas Academy of Science* 56:206–211.
- von Helversen, O., and D. von Helversen. 1994. The “advertisement song” of the lesser noctule bat (*Nyctalus leisleri*). *Folia Zoologica* 43:331–338.
- Wilkinson, G. S., and G. F. McCracken. 2003. Bats and balls: sexual selection and sperm competition in the Chiroptera. Pages 128–155 in T. H. Kunz and M. B. Fenton, editors. *Bat ecology*. University of Chicago Press, Chicago, Illinois, USA.
- Williams, D. F., and J. S. Findley. 1979. Sexual size dimorphism in vespertilionid bats. *American Midland Naturalist* 102:113–126.
- Zagmajster, M. 2003. Display song of parti-coloured bat *Vespertilio murinus* Linnaeus, 1758 (Chiroptera, Mammalia) in southern Slovenia and preliminary study of its variability. *Natura Sloveniae* 5:27–41.

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