THERYA, abril, 2013
Vol.4(1):69-78
DOI: 10.12933/therya-13-109

Acoustic monitoring of bats, considerations of options for long-term monitoring

Winifred F. Frick[1]

Abstract

Acoustic recording of echolocation activity of bats is a means of monitoring bat activity or habitat use over time and space. Advances in technology permit long-term monitoring of echolocation activity relatively cheaply and there is much interest in developing acoustic monitoring protocols for long-term monitoring of bat populations. There are many challenges to using acoustic recordings for monitoring underlying changes in bat populations, but acoustic recordings can be used to evaluate changes in use and activity. There has been much recent attention and effort to develop automated species identification/classification and to make these tools available through both commercial software or free online. More work needs to be done, however, before automated species classification can be implemented for monitoring bats on continental or global scales. Here, I provide a brief overview of current popular systems for long-term echolocation monitoring and discuss some of the challenges and advantages of current acoustic monitoring systems.

Key words: bats, detector systems, echolocation activity, acoustic monitoring, ultrasonic signals.

Resumen

La detección de los pulsos de ecolocalización permite monitorear la actividad de los murciélagos y/o su uso del hábitat a través del tiempo y del espacio. Los avances tecnológicos recientes permiten desarrollar monitoreo de ecolocalización a largo plazo de forma relativamente barata; existe interés en el desarrollo de protocolos de monitoreo acústico para el seguimiento a largo plazo de las poblaciones de murciélagos. Son muchos los desafíos que presenta la aplicación de la detección acústica para evaluar los cambios en las poblaciones de murciélagos, pero esta técnica se puede utilizar para evaluar los cambios en el uso del hábitat y la actividad del ensamble de especies de murciélagos. Recientemente ha habido mucha atención y esfuerzos para desarrollar herramientas automatizados de identificación / clasificación de especies y hacerlas disponibles a través de software comercial o en línea de forma gratuita. Se requiere aun mucho trabajo antes de que sea posible la clasificación automatizada de las especies y el monitoreo de murciélagos a escala continental o global. A continuación, se presenta una breve descripción de algunos sistemas populares para el monitoreo de la ecolocalización a largo plazo, discutiendo algunas de sus ventajas y desventajas.

[1]Department of Ecology and Evolutionary Biology, University of California, Santa Cruz, Santa Cruz, USA 95064. E-mail wfrick@ucsc.edu (WF)

Palabras clave: detectores ultrasónicos, ecolocalización, monitoreo acústico, murciélagos, señales ultrasónicas, sistemas de detección.

Introduction

Bats are cryptic, nocturnal mammals that are often difficult to study. In particular, monitoring population trends of bats presents considerable challenges because standard wildlife management methods for estimating population sizes or densities on the landscape are often not feasible. Yet monitoring bats is a high priority given the important role they play in ecosystems and their potential sensitivity to both land-use and global climate change (Jones *et al*. 2009).

Technological advancements in acoustic detector systems and computer hardware accessories permit recording echolocation calls emitted by bats as a means of monitoring bat echolocation activity. Bats use echolocation to find insect prey and these echolocation calls can be detected with high frequency microphones and recorded onto storage media for later analysis with computer software packages. There are a number of different methods and systems for acoustic monitoring of bat echolocation activity and each system has advantages and disadvantages depending on the goals and objectives of a project (Parsons and Szewczak 2009).

In contrast to the way in which songbirds produce complex and unique call signatures during mating displays, bats use echolocation sound primarily for detecting prey. Therefore, there can be considerable inter-species overlap in echolocation call morphologies based on foraging strategies and diet preferences. There is also considerable intra-species and even intra-individual variation in echolocation properties based on habitat type and foraging mode (Hayes *et al*. 2009). The inter-species overlap and intra-species variation in bat echolocation signatures make automated species-specific call identification challenging (Hayes *et al*. 2009; Parsons and Szewczak 2009). Sophisticated multi-variate statistical methods, such as neural networks and discriminant function analyses, have permitted development of automated call classification algorithms to be incorporated into software packages for call identification (Parsons and Jones 2009; Walters *et al*. 2012). These analytical tools have improved the feasibility of using acoustic monitoring for tracking spatio-temporal changes in bat activity by species or species groups with a repeatable, automated post-processing data management flow. Although variation in species echolocation call morphologies may never permit absolute certainty in species identification, having a repeatable automated classification system provides a reasonable means for assessing bat use of habitats through time and with expected further advancements in acoustic monitoring technologies, identification will likely become more accurate in the future.

Acoustic monitoring is a well-established method for monitoring bat activity patterns and changes in habitat use and activity of bats across habitats (Hayes 1997; 2000; Broders 2003; Gehrt and Chelsvig 2003; Gehrt and Chelsvig 2004; Gorresen *et al*. 2008; Hayes *et al*. 2009; Parsons and Szewczak 2009). The relationship between bat echolocation activity and abundance of bats has not been conveniently evaluated and at this time cannot be used to directly infer population densities (Hayes *et al*. 2009). A classic conundrum is whether, for instance, 10 bat passes represent 10 bats flying by the detector or one bat passing by 10 times.

Acoustic activity indices (Miller 2001) can be used in lieu of counting bat passes to provide a simple and less biased means to quantify bat activity. Acoustic activity indices generally use a presence/absence of a call within a defined temporal interval (*e.g*. 1 minute; Miller 2001). In general, researchers tend to equate higher levels of bat activity with higher quality habitat; however, density (or in this case activity) is not always a good indicator of habitat quality (Van Horne 1983).

Acoustic monitoring provides information on the level of use of a habitat by bats. It is reasonable to assume that sites with greater levels of bat activity receive greater use by bats than sites with less bat activity. It is also reasonable to assume that changes in activity over time equates to changes in use of those habitats over time. These changes may be due to underlying changes in populations and provide an index of the status of a population although the causal mechanisms for such changes may not always be clear. In order for echolocation monitoring to be useful for assessing changes in relative use of different habitats and over time, it is necessary to have proper replication (at the appropriate spatial and temporal scales) of sampled sites and a valid study design (Hayes *et al*. 2009).

Echolocation data vary greatly both spatially and temporally. Changes in nightly conditions such as temperature, humidity, and relative insect availability influence the amount of nightly bat activity (Hayes 1997). Hayes (1997) recommends approximately six nights of recording per site to account for night-to-night variation in echolocation activity. Likewise, individual heterogeneity in site characteristics can influence the amount of variation.

Therefore, replication is needed within habitat types in order to have a proper scope of inference to assess differences in bat use of habitats. High spatio-temporal variation in data can reduce statistical power to detect biologically significant differences in use either among habitats or across time. A monitoring program should encompass enough spatial and temporal replication to account for high variability and permit enough statistical power to make meaningful comparisons for the stated objectives of comparing use among habitats through time.

Acoustic Monitoring Systems

There are currently several options for long-term acoustic monitoring that involve either hardware components or software options for analyzing bat calls. I discuss here three systems for long-term acoustic monitoring based on my familiarity with these options. The reader is advised that other options are available and should be carefully considered before deciding which system best fits their research needs. The systems discussed here are not meant to be an exhaustive review of all available options. The three systems discussed here, include 1) Anabat detecting and recording system by Titley electronics (www.titley.com.au). 2) the AR125 detector and FR125 field recorder by Binary Acoustic Technology (BAT; www.binaryacoustictech.com); and 3) Song Meter SM2BAT+ detector/recorder by Wildlife Acoustics (www.wildlifeacoustics.com). These systems provide the necessary hardware for detecting the ultrasonic frequencies of bats and recording them onto a storage media for later analysis on a computer. The process of recording echolocation calls may require transforming the high-frequency sound as well as recording that sound in a digital or analog format (Parsons and Szewczak 2009).

There are several methods for transforming high frequency sound. The details can be found in (Parsons and Szewczak 2009). For designing an effective acoustic monitoring system, it is necessary to determine the appropriate and cost-effective hardware and the software analysis tools that will be useful for subsequent analysis of the bat activity. This requires an understanding of the differences in methods of transforming and storing high-frequency sound.

Anabat. The Anabat hardware uses a frequency-division system for transforming the high frequency sound by reducing the number of cycles. The advantages of frequency division include: 1) it records/operates in real time; 2) it is broadband and can detect/record across the entire range of frequencies that an ensemble of bats may use (Parsons and Szewczak 2009); 3) it retains most of the time and frequency information for calls; and 4) is not memory intensive because it reduces the information in each call to frequency versus time.

Frequency division is compatible with zero-crossing analysis that displays the frequency-divided calls in a time versus frequency graphical display for visualization and analysis.

The main disadvantages of the frequency division system coupled with zero-crossing analysis of Anabat are that it only detects the harmonic with the greatest energy and do not retain the information on the amplitude structure of the call, which may be important for species identification. It may also cut the initial and final parts of the calls because it uses an intensity threshold for the detection (*e.g*. Fenton 2000). The final result might not be an accurate representation of the call, but still may contain enough information for the identification of the species. Anabat may also be considerably less sensitive than systems based on direct digitalization (Adams *et al*. 2012). Until recent improvements in storage media capabilities and processor speeds, the Anabat system was the only viable option for long-term field deployment for real-time recordings of bat activity. Thus, many past efforts have used frequency-division and zero-crossing analysis for monitoring bat activity and developing call libraries. The analysis software for analyzing Anabat calls is based on free-ware written by Chris Corben (Analook or AnalookW). Documentation and freeware downloads can be found at http://users.lmi.net/corben/anabat.htm. Zero-crossing analysis can be used with species identification algorithms either through Analook, or through third party systems (*e.g.* Bat Call IDentification). BCID is a program compatible with Analook that uses zero-crossing data for automated species identification. It performs quite well compared to Sonobat 3's classification algorithms, but is currently only available for eastern North American bat species (http://www.batcallid.com/).

*B.A.T. and Song Meter SM2***.** Both the Binary Acoustics Technology (B.A.T.) and Song Meter SM2BAT+ systems use a direct recording system that digitalizes at high sampling speed the full-spectrum sound onto storage media. The advantages of these systems for direct recorded, full-spectrum include: 1) recording/operating in real-time; 2) they use broadband microphones that detect/record across the entire range of frequencies that an ensemble of bats may use (Parsons and Szewczak 2009); and 3) they retain all the sound information, including amplitude and information about harmonics, which in many cases gives you more parameters to use for multivariate algorithms for species identification. However, whether additional parameters improve automated species identification has not been empirically demonstrated. The ability to directly record full spectrum sound in real time was a major breakthrough for acoustic monitoring of bats because previously there was a significant trade-off between using Anabat for greater temporal sampling (real time) but only retaining the frequency versus time information for analysis versus a time-expansion recording that was not capable of real-time recording but retained the full-spectrum sound (Parsons and Szewczak 2009). The main disadvantage of real-time recordings of full spectrum sound is that it requires much greater memory storage, but high capacity memory storage media (*e.g.* secure digital [SD] cards and Universal Serial Bus [USB] drives) are now available at relatively low cost.

The Song Meter SM2BAT+ system is currently the most flexible commercial product as it directly records full spectrum sound as well as can directly record in zero-crossings or convert full-spectrum sound to zero-crossings depending on user preference. Zero-crossing compatibility is useful if reliable automated detection algorithms using zero-crossings are available (*e.g.* in eastern North America) or for comparing with other monitoring projects that use this system. However, the comparison of relative bat activity across detecting/recoding platforms is not advised due to the likely bias in detectability based on hardware differences among microphones and detectors (*e.g.* Adams *et al*. 2012). These differences include the relative sensitivity of the microphones and the fact that Song Meter SM2BAT+ microphones are omnidirectional, whereas Anabat microphones are not.

The descriptions above focus on systems designed for long-term acoustic monitoring. Several of these companies also make units suitable for hand-held or active acoustic monitoring, such as the Echo Meter (EM3+) by Wildlife Acoustics or Anabat SD2 active monitoring kit. Active acoustic monitoring should be used to record echolocation calls on release from capture to build a reference echolocation library (O'Farrell *et al*. 1999). An accurate reference library built from hand-released identified bats is the basis for all automated species identification training algorithms as well as training human observers for accurate identification of calls. Active monitoring can also be used with driving or walking transects, depending on study objectives and needs.

Automated Call Analysis

Automated species identification is an area of active research and tool development. Automated species identification requires two major steps: 1) recognizing a bat call from background noise and accurately measuring call parameters of interest; 2) using measured call parameters in a multivariate analysis for classifying a call to a given species. Walters *et al*. (2012) demonstrated the need for standardized protocols to permit comparability for broad scale and long-term monitoring and advocates for free online tools for call processing. Here, I describe what is currently available in North America, but note that future developments in this area are rapid.

Sonobat 3 is a commercially available software package that has an automated call detection and measuring tool and built-in species identification filters for bat species in different geographic areas of the United States (but not for Mexico). Sonobat requires use of full-spectrum recordings and therefore is not compatible with Anabat recordings. Sonobat was designed to work with recordings made with Pettersson microphones and the BAT system, which have very low levels of noise. A new release of Sonobat has resolved certain issues with visualizing bat calls from SongMeter recordings, which have more background noise than Pettersson detectors due to differences in microphone design and components (Szewczak, personal communication). The current version of Sonobat resolves better visualization of calls recorded with SongMeter, but performance of automated identification of species is still being improved and tested. This is an area of active development and it is anticipated that improvements will continue into the future.

According to current field tests, version 3.1 of Sonobat, which uses a compensation filter for post-processing resolution of the frequency response of SongMeter microphones, performs equally well to recordings made with Pettersson detectors or the B.A.T. system for bats that are within close range of the microphone (Szewczak, personal communication). For calls that are recorded at the edge of the microphone detection range, the signal to noise ratio is sufficiently high to currently obscure sufficient resolution for positive species identification. Such calls can be classified into broad groups of low-frequency calls (so called LoBat) or high-frequency calls (HiBat), but may not be identifiable to species level. Therefore, these more distant recordings are useful for monitoring overall bat activity levels, but are not of sufficient quality for species identification. This may produce the appearance of unsatisfactory low levels of species identification if there is a large ratio of distant (lower quality) calls to closer (higher quality) calls. However, restricting species-level monitoring to closer calls that are of sufficiently high quality for species identification (*i.e.* ignoring poorer-quality distant calls) should produce a reliable means for tracking trends in species-level bat activity through time. In effect, the range of the microphone is smaller for identifying species than it is for identifying overall bat activity. Note, however, that if automated processing algorithms change in the future for better processing of distant calls, observer bias will be introduced into studies that aim to measure long-term trends in bat activity across years as it will essentially increase the range of detection of identifiable calls. If significant changes are made to automated species classification, data should be analyzed using the same system to avoid introducing observer bias.

Table 1. Comparison of three commercial acoustic systems for long-term acoustic monitoring of bats

System Type	*Advantages*	*Disadvantages*
Anabat	- Low memory usage - Easily adjust settings - Fewer noise files - Analysis software is freeware	- Expensive - Not weatherproof - Only zero-crossings
BAT	- Data easy to download - Microphone sensitive - Full spectrum/Sonobat compatible - Ability to send data electronically where cell phone reception occurs for long-term monitoring	- Expensive - Memory intensive - Power consumptive - Not weatherproof - Multi-piece
Song Meter SM2BAT+	- Least expensive - One piece of equipment - Weatherproof - Sensitive omnidirectional microphone - Temp logger can be incorporated - Flexible recording schedule - Full spectrum or zero-crossing compatible	- Memory intensive - Noiser microphone leads to fewer recorded calls identified to species by Sonobat (compared to Pettersson's microphones)

Wildlife Acoustics recently announced a commercial release of their own automated species identification program: Kaleidoscope Pro. The initial release includes classifiers for 20 species in North America and 10 species in the United Kingdom. This new system has not yet been tested by independent researchers. There are other commercially available software packages (*e.g*. Raven, BatSound, Avisoft, SasLab) that can be used for visualizing and measure call parameters from bats. To date, only Kaleidoscope and Sonobat have a built in automated species identification tools; AnalookW software allows the automated measuring of many call parameters and call sequence data of Anabat zero-crossing files, but does not currently implement an automated identification tool. AnalookW can be complemented with the species identification tool of BCID for bats in eastern North America (http://www.batcallid.com/).

Survey Implementation Considerations

Nightly Temporal Sampling. The standard protocol for recording bat echolocation calls typically involves recording from sunset to sunrise. This sampling scheme is based more on the fact that the default recording system for long-term acoustic monitoring was the Anabat system that had simple all-night recording scheduling rules and was not memory or power consumptive. The Song Meter SM2 system and other recording systems such as Avisoft Recorder, permit a more flexible recording schedule that are capable of sub-sampling recorded times throughout the night (*e.g.* record 10 minutes of every hour).

The advantage of all-night recording is that you have sampled the bat activity for a given night and have a complete record of activity on each sampled night. The disadvantage of recording all night activity is that for full-spectrum direct recordings, this is memory and power consumptive. Manually analyzing recordings, without automated measuring or automated identification tools, may require an inordinate amount of time. Until studies indicating whether a temporal sub-sampling scheme within a night produces comparable estimates of bat activity to all night sampling, an all-night sampling schedule is recommended. However, analysis of pilot data to compare results from all night sampling to within-night sub-sampling could be useful to determine if sub-sampling is sufficient for characterizing bat activity patterns across habitats for target species. Some species of bats may concentrate activity in very short periods at the beginning and the end of the night, making irrelevant an all-night sampling (*e.g*. *Molossus* spp.; Holland *et al*. 2011). Clearly, study objectives should drive the appropriate research design in setting up a temporal monitoring scheme.

Conditions for Highest Quality Field Recordings of Ultrasonic Signals. To maximize call quality for species identification, it is advisable to place the microphone in situations that avoid and reduce background noise and distortion effects. Placement of the microphone also depends on study objectives and placement in open settings away from clutter may bias the species composition of species detected. The Sonobat website (www.sonobat.com) has a detailed section of "Recording Advice" which includes the following advice:

1. Place microphone at least 1 – 2 meters above ground, to reduce surface echoes, avoid thermal layering, or near-ground air convection currents, which can distort ultrasound signals.
2. Place microphone in open 'flyways' and away from clutter
3. Avoid placing microphones next to large echo-producing surfaces, such as asphalt, building facades, bridge structural surfaces, flat water, etc. These considerations are likely more important for recording in full-spectrum than if using frequency-division. Placing the detector in open areas at higher heights above

the ground (*e.g.* > 5.5 meters/ 18 feet) should effectively increase the sample volume with an omnidirectional microphone. As most bats aren't expected to fly much below 2 meters, a microphone at that height will be sampling areas that bats can't realistically be expected to fly. An exception is trawling bats that fly low above water and understory aerial insectivores such as *Pteronotus parnellii*. In addition, placing the microphone at higher heights above ground and in open settings will also increase the chance that recorded calls will be longer duration/search phase calls typical of bats in open-air flight. These calls typically provide greater information content associated with higher species-discrimination confidence (www.sonobat.com).

Data Analysis for Monitoring Trends in Bat Activity. The basic unit of measurement for assessing bat activity is the number of bat passes per species (or species group) per some unit time (usually by night). Acoustic data are not usually normally distributed and therefore do not conform to the assumptions of normality and equal variance imposed by standard statistical tests like an analysis of variance (ANOVA). For monitoring purposes, analyses of data to compare mean number of bat passes among habitat types or years can be accomplished by transforming the bat passes response variable by a log transformation or by using more sophisticated statistical tests that assume a different underlying distribution of the response variable (*i.e.* Generalized Linear Models – GLMs).

Acoustic data are notoriously "noisy", meaning that there is high night-to-night variation in the amount of bat activity (Hayes 1997). This type of noisy variability can often make detecting statistically or biologically significant differences challenging. Environmental variables can be included as covariates within a statistical modeling framework to account for variation caused by identified factors and allow for a more robust test for biologically and statistically significant differences. Covariates such as a nightly minimum temperature, maximum nightly wind speed, and moon phase can be included and tested using a model selection framework, such as Akaike's Information Criteria (AIC). AIC measures the relative fit of a model given the set of candidate models and can be used to assess which parameters do the best job in explaining the variation in the data (Burnham and Anderson 2002). To use AIC model selection effectively, it is important to clearly define a set of *a priori* candidate models that correspond to biological hypotheses about the system of interest.

Training Opportunities. Researchers embarking on implementing acoustic monitoring techniques should investigate training or workshop opportunities to become familiar with the technologies available for recording and data processing as well as background on bat echolocation. There are several training options available, including system-specific training workshops held by companies such as Wildlife Acoustics and Titley Electronics. Cori Lausen currently offers training workshops in both Anabat/AnalookW platforms and SongMeter Bat+ platforms (http://www.batsrus.ca/training.html). Bat Conservation International also provides acoustic monitoring workshops that include information on multiple different recording/processing platforms (www.batcon.org).

Conclusions

Use of acoustic monitoring for bat research has grown substantially over the past few decades. The ability to record and store large amounts of echolocation data in the field has greatly increased ability to monitor activity of bats across space and time. However, our ability to accurately identify species from echolocation data and interpret biological meaning behind differences in echolocation activity is still playing catch-up to some degree. Automated species identification is an area of exciting and rapid progress that is seeing both commercial and open-source development, which will propel the field even further forward. Standardizing systems and building a common framework for analyzing and interpreting echolocation data will aid efforts to build a global bat monitoring program.

Acknowledgements

I thank P. Cortés-Calva for the invitation to write this article. Three anonymous reviewers provided helpful feedback on the manuscript. Funding provided by National Science Foundation DEB-1115895.

Literature Cited

Adams, A. M., M. K. Jantzen, R. M. Hamilton, and M. B. Fenton. 2012. Do you hear what I hear? Implications of detector selection for acoustic monitoring of bats. Methods in Ecology and Evolution 3:992-998.

Broders, H. 2003. Another quantitative measure of bat species activity and sampling intensity considerations for the design of ultrasonic monitoring studies. Acta Chiropterologica **5**:235-241.

Burnham, K., P., and D. R. Anderson. 2002. Model selection and multimodel inference: a practical information-theoretic approach. Springer, EE.UU.

Gehrt, S. D., and J. E. Chelsvig. 2003. Bat activity in an urban landscape: patterns at the landscape and microhabitat scale. Ecological Applications 13:939-950.

Gehrt, S. D., and J. E. Chelsvig. 2004. Species-specific patterns of bat activity in an urban landscape. Ecological Applications 14:625-635.

Gorresen, P., A. Miles, C. Todd, F. Bonaccorso, and T. Weller. 2008. Assessing bat detectability and occupancy with multiple automated echolocation detectors. Journal of Mammalogy 89:11-17.

Fenton, M. B. 2000. Choosing the 'corrrect' bat detector. Acta Chiropterologica 2:215-224.

Hayes, J. P. 1997. Temporal variation in activity of bats and the design of echolocation-monitoring studies. Journal of Mammalogy 78:514-524.

Hayes, J. P. 2000. Assumptions and practical considerations in the design and interpretation of echolocation-monitoring studies. Acta Chiropterologica 2:225-236.

Hayes, J. P., H. K. Ober, and R. E. Sherwin. 2009. Survey and monitoring of bats. Pp. 112-132 inThe Ecological and Behavioral Methods for the Study of Bats (Kunz, T. H., and S. Parsons, eds.). The John Hopkins University Press. Baltimore, EE.UU.

Holland, R. A., C. F. J. Meyer, E. K. V. Kalko, R. Kays, and M. Wilkelski. 2011. Emergence Time and Foraging Activity in Pallas' Mastiff Bat, *Molossus molossus* (Chiroptera: Molossidae) in Relation to Sunset/Sunrise and Phase of the Moon. Acta Chiropterologica 13:399-404.

Jones, G., D. S. Jacobs, T. H. Kunz, M. R. Willig, and P. A. Racey. 2009. Carpe noctem: the importance of bats as bioindicators. Endangered Species Research 8:93-115.

Miller, B. W. 2001. A method for determining relative activity of free flying bats using a new activity index for acoustic monitoring. Acta Chiropterologica 3:93-105.

Norberg, U. M., and J. M. V. Rayner. 1987. Ecological morphology and flight in bats (mammalia; chiroptera): wing adaptations, flight performance, foraging strategy and echolocation. Philosophical Transactions of the Royal Society of London Series B-Biological Sciences 316:337-419.

O'Farrell, M. J., B. W. Miller, and W. L. Gannon. 1999. Qualitative identification of free-flying bats using the Anabat detector. Journal of Mammalogy 80:11-23.

Parsons, S., and G. Jones. 2009. Acoustic identification of twelve species of echolocating bat by discriminant function analysis and artificial nerual networks. The Journal of Experimental Biology 203:2641-2656.

Parsons, S., and J. M. Szewczak. 2009. Detecting, Recording, and Analyzing the Vocalizations of Bats. Pp. 91-111 in Ecological and Behavioral Methods for the Study of Bats (Kunz, T. H., and S. Parsons, eds.). The John Hopkins University Press. Baltimore, EE.UU.

Schnitzler, H. U., and E. K. V. Kalko. 2001. Echolocation by insect-eating bats. Bioscience 51:557-569.

Simmons, J. A., M. B. Fenton, and M. J. O'Farrell. 1979. Echolocation and pursuit of prey by bats. Science 203:16-21.

Van Horne, B. 1983. Density as a misleading indicator of habitat quality. The Journal of Wildlife Management 47:893-901.

Walters, C. L., R. Freeman, A. Collen, C. Dietz, M. B. Fenton, G. Jones, M. K. Obrist, S. J. Puechmaille, T. Sattler, B. M. Siemers, S. Parsons, and K. E. Jones. 2012. A continental-scale tool for acoustic identification of European bats. Journal of Applied Ecology 49:1064-1074.

Sometido: 18 de febrero de 2013
Revisado: 6 de abril de 2013
Aceptado: 18 de abril de 2013
Editor asociado: Patricia Cortés-Calva
Diseño gráfico editorial: Gerardo Hernández