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Methods for Assessing Colony Size, Population Size, and Relative Abundance of Bats

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ONE OF THE FIRST QUESTIONS asked by nearly everyone when they first visit a new city, state, or country is, "How many people live here?" Human demographers are interested in this population statistic because it provides important information needed to assess the distribution and use of resources and commodities for sustaining these municipalities. Community leaders are interested in knowing the population size of organizations needed to maintain public health, safety, and educational institutions. The same can be stated for smaller units such as families, schools, corporations, and other entities that impact local economies. Ecologists are similarly interested in how changes in population size might impact the availability of food and other resources needed to sustain natural ecosystems.

When estimating the abundance of organisms, including humans, it is important to distinguish between the number of individuals present in a discrete area or habitat from the number of individuals present at some larger spatial scale. For bats, these scales may include number of individuals that roost in a particular tree cavity or cave, the size of a population on an island or one that occupies a forest patch, the total number of individuals of a species in existence, or its effective population size.

Traditionally, a population is defined as a group of individuals of a single species that inhabits a specific area during a specified period of time. Such populations have natural boundaries, but for practical reasons the boundaries are more often defined by the investigator. Underlying this concept is the assumption that all individuals that comprise such populations represent breeding or potentially breeding units. In practice, however, this assumption is seldom tested directly. When the numbers of organisms in demographic populations are estimated, most models assume the absence of immigration, emigration, births, or deaths.

For many species, it may not be practical to census or estimate the number of individuals present in a particular habitat or region. Thus, indices of abundance are often used to assess relative changes in colony size or changes in abundance over time and space. However, it should be noted that these indices provide little or no information on actual colony or population size. Notwithstanding, from a practical perspective, it may be easiest to determine relative abundance of organisms present by comparing numbers captured or detected at different times and places.

Censusing or estimating numbers of organisms present in discrete situations (e.g., cave or tree cavities) may be relatively easy for species that exhibit high fidelity to such places. However, for other species that move frequently among different roosts and form fission-fusion societies, estimating numbers in a colony poses additional challenges.

We define a colony as a discrete group of bats that forms a social unit during a specific period that is either limited to a specific site, such a cave or tree cavity, or that shares several adjacent roosts between which regular exchanges occur. Because most bat species are highly mobile, colony type may vary seasonally, based on different life-history stages, such as during maternity, transient, swarming, and hibernating periods.

We define a population as a group of breeding or potentially breeding individuals of the same species present at the same time and specified place. A population of bats may be comprised of several individuals or colonies of varying size and distribution during a specified period of time. From an evolutionary perspective, a species may be represented by one large panmictic population, or it may be subdivided into several discrete demes or local breeding units that may change in size and composition over time. Historically, some forest-dwelling species may have had contiguous distributions, but naturally occurring events, such as glaciations and more recent anthropogenic changes, have isolated some populations. Similarly, founder populations isolated on islands are considered discrete units for assessing both demographic population size and effective population size.

ESTIMATING NUMBERS OF BATS

Whether bats roost in enclosed spaces such as caves and tree cavities or in open foliage, observability and detectability are the most common challenges faced by researchers interested in estimating numbers present in colonies or in populations. A second challenge is the limitation of time and money needed to obtain reliable estimates of colony and population size (Nichols and Conroy, 1996). In general, several methods have been used to estimate numbers of animals, each of which shares challenges and underlying assumptions (Nichols and Conroy, 1996; Braun,

2005). Determining the number of animals present in a particular area (a census) can be achieved by directly counting all animals present, or alternatively, by making an estimate based on some probability that only a proportion of animals will be detected, observed, or captured. In most cases, it may not be possible to count all bats present in a particular study colony or study area, except perhaps in situations when bats emerge nightly from traditional roosts. Estimating numbers of bats that comprise an entire population inevitably will require both intensive and extensive sampling efforts and then evaluation of the associated assumptions of stated methods.

In this chapter, we first provide a conceptual framework for determining animal abundance and then review methods that have proven valuable for estimating numbers of bats present in different environments (e.g., roosts foraging habitats, regions, and ranges). We distinguish between a census or colony count, population estimate, and indices of abundance. We also discuss the strengths and limitations of each method.

CONCEPTUAL FRAMEWORK

Censusing Colonies and Populations

A census is a complete count or estimate that involves the determination of colony or population size (N) in a particular habitat or area directly from the number of animals counted (C), making corrections for sampling bias (α) or observation probabilities (β), where $N=C$ (Jarman et al., 1996). Assumptions necessary for estimating C are: (1) the sampling fraction equals one ($\alpha=1$), (2) the observability equals one ($\beta=1$), and (3) the population is closed. The first assumption requires that a designated survey area can be searched and that all individuals present will be recorded. The second assumption requires that all animals are detected (typically by visual means) and counted, and that no individuals are counted more than once. The third assumption requires that the census be conducted over a sufficiently short interval so that no immigration, emigration, births, or deaths occur during the census period (Jarman et al., 1996).

Statistical Estimates

Statistical estimates of abundance rely on count statistics, including an estimation of observation probability and sampling protocols. For example, if C denotes a count statistic, N is an estimate of number of animals present in a colony or population (quantity of interest), and β is the observation probability, then $E(C)=\beta N$, where $E(C)$ denotes the expected mean value of the count statistic. The term β is the probability that an individual animal in a colony or population (N) will appear in the count statistic (C). Assuming that β can be reliably estimated, \hat{N} can be estimated using the equation $\hat{N}=C/\beta$. For example, if 40 bats are captured in a harp trap placed at the opening of

a cave ($C=40$), and if we assume that only half of the bats were captured ($\beta=0.50$), then an estimate of the total number of bats present in the cave would be expressed as $N=40/0.50=80$.

To estimate the size of a bat population that includes several cave or tree colonies in a specified area, one would need to sample a spatial unit that represents some fraction (α) of the total area or number of caves or trees of interest. The total number of animals present (N) can be estimated from the number of animals counted (N), where $\hat{N}=N/\alpha$ (hats denote estimates). If 40 bats (N) occupied a single sample location (cave), representing a proportion (20%) of some larger area of interest (other caves), then one can estimate the number of bats present in the total area as $\hat{N}=40/0.20=200$.

Concepts of observability and spatial sampling can be combined into a single estimator, using the equation $N=C/(\alpha\beta)$, where C is the count statistic, β is observation probability, and α is the fraction of animals present in a sample unit. From the above example, where $C=40$, $\beta=0.50$, and $\alpha=0.20$, the total estimated population would be $\hat{N}=40/(0.50\times 0.20)=400$. In principle, virtually all estimators of animal abundance can be expressed in the form of this simple equation (Nichols and Conroy, 1996).

Estimates of sample variance are required for determining how close a statistical estimate may be to some true abundance. Methods for estimating sample variance are beyond the scope of this chapter, and thus readers are advised to consult statistical references that explicitly address this topic (e.g., Nichols and Pollock, 1983; Skalski and Robson, 1992; Lancia et al., 1994; Nichols and Conroy, 1996).

COLONY VERSUS POPULATION ESTIMATES

Knowledge of baseline population levels, population structure, and genetic diversity are needed for most any aspect of life-history analysis. Much of our current understanding of population trends in bats is based on observations of changes in colony sizes over time (Ellison et al., 2003). This information is mostly derived from repeated visits to single roosts to count bats emerging at dusk (Kunz and Anthony, 1996; Choate and Anderson, 1997; Hoying and Kunz, 1998; Warren and Witter, 2002; Hristov et al., 2008; Hristov et al., in press). But because bat populations often consist of individuals distributed among different roosts, assessing changes in abundance at a single roost may lead to biased estimates of population trends (Sherwin et al., 2003; Sherwin and Altenbach, 2004). For example, observed increases in the number of bridge colonies appear to coincide with observed decreases in the sizes of some cave colonies of Brazilian free-tailed bats in the southwestern U.S. (Horn and Kunz, 2008).

To reliably estimate regional trends in bat populations, researchers should (1) establish geographic limits of the region being considered, (2) determine the number and sizes of roosts in the region, (3) locate all roosts in the region, (4) determine daily and seasonal dispersal distances within the limits of the region, and (5) determine rates of immigration and emigration to the region (Thomas and LaVal, 1988). It also is important for researchers to understand basic assumptions that underlie population models (Hayes et al., this volume), and, clearly articulate these assumptions before conducting population estimates. Intensive, long-term research using different research and monitoring protocols and methods is necessary to satisfy these assumptions (O'Shea et al., 2004; Hayes et al., this volume).

DEMOGRAPHIC METHODS FOR ASSESSING ABUNDANCE OF BATS

Methods suitable for assessing abundance of bats vary depending on size and mobility of the species, relative numbers of individuals present, access of investigators to roosting sites, and the applicability, availability, and reliability of devices that are used (Mitchell-Jones, 1987; Kunz and Kurta, 1988; Thomas and LaVal, 1988; Frantz, 1989; Sabol and Hudson, 1995; Kunz et al., 1996a, 1996b; Frank et al., 2003; Kunz, 2003; O'Shea and Bogan, 2003; Betke et al., 2008; Horn and Kunz, 2008; Hristov et al., 2008).

Basic knowledge of a species' life-history characteristics is important before selecting methods for studying it. This knowledge should include a general understanding of roosting habits, nightly emergence behavior, seasonal behavior, and how biotic and environmental factors may affect local abundance and distribution. Knowledge of temporal and spatial activity associated with a particular species or population is also important. If devices such as binoculars, video cameras, night vision devices, reflectance or thermal infrared cameras, motion detectors, ultrasonic detectors, or radar are used to extend the sensory capabilities of an observer for censusing or estimating abundance, researchers must be thoroughly familiar with their operation, limitations, and potential biases (Kunz et al., 1996b; Kunz, 2004).

Roost sites that are relatively easy to locate and those that house relatively small to moderately sized colonies of bats (fewer than 1,000 individuals) offer the greatest potential for conducting reliable estimates of colony size (e.g., Swift and Racey, 1983; Kunz and Anthony, 1996; Hoying and Kunz, 1998; O'Donnell, 2000; Vonhof and Fenton, 2004; Hayes et al., this volume). Species that roost alone or in small groups in foliage, rock crevices, and tree cavities (Kunz and Lumsden, 2003; Barclay and Kurta, 2007) and those that form large colonies pose the greatest challenges for reliable censusing (Davis et al., 1962; Constantine, 1966; Humphrey, 1971; Sabol and Hudson, 1995; Bogan

et al., 2003; Frank et al., 2003; O'Shea and Bogan, 2003; Hayes et al., this volume).

Censusing Bat Colonies

Historically, four methods have been used for censusing bat colonies: roost counts, evening emergence counts, evening dispersal counts, and disturbance counts (Kunz et al., 1996b; Kunz, 2003; O'Shea and Bogan, 2003). In general, accurate and reliable estimates of the actual number of bats present in roosting situations are seldom feasible except for relatively small, gregarious species. Highly gregarious species often require the coordinated efforts of several researchers and/or the use of sophisticated imaging devices. Also, some species are highly susceptible to disturbance in roosting situations and may abandon these sites in response to censusing efforts (Tuttle, 1979, 2003). In other situations, lack of observer access to a roost or low visibility at the time of emergence may preclude a reliable census or estimate.

In situations where direct access to the interior of a bat roost is precluded or inadvisable (based on physical challenges or safety risks to observers), evening emergence counts offer the best alternative for censusing bats (Kunz and Anthony, 1996; Hoying and Kunz, 1998). Disturbance counts may be of value in some limited situations (Racey, 1979), but in general they are not reliable and in fact may increase risks of mortality, especially to nonvolant young.

Roost Counts

Some bat species can be observed and counted directly in their roosting sites. The relatively high fidelity that bats exhibit to such roosts (Kunz, 1982; Lewis, 1995) often makes it possible to estimate colony size by direct observation (Kunz, 2003; Kunz and Reynolds, 2003; McCracken, 2003;

Tuttle, 2003). In some instances, a single observer can count the number of roosting bats, although making reliable counts under these circumstances often involves making several assumptions. For example, it is commonly assumed that all bats are readily observable in roosts (Kunz, 2003). Efforts to infer population trends by comparing current and historical estimates of roosting bats are often based on the invalid assumption that availability and quality of roosts is static and that bats exhibit high rates of fidelity to roosts through time (Sherwin and Altenbach, 2004; Hayes et al., this volume).

Reliable visual censuses or estimates of large, active colonies of cave-roosting bats pose several challenges. Estimates of cluster density averaged from capture or photographic methods (Fig. 7.1A) have been used to extrapolate to the total area occupied by roosting bats (Constantine, 1967; Tuttle, 1979, 2003). However, this approach may cause considerable disturbance to roosting bats, especially during maternity periods. Moreover, irregularities in roost substrates, variations in cluster density, and dispersion (Fig. 7.1B) can lead to biased estimates when cluster densities are extrapolated to areas that are not uniformly distributed on the roost substrate. At best, this method will yield reasonable estimates of colony size, and at worst, estimates only in orders of magnitude.

In some roosting situations where a species forms small, compact, clusters, direct visual counts can provide reliable abundance data on colony size (Fig. 7.2A; Tuttle, 1979; Hoying and Kunz, 1998). In other situations, where the probability of disturbing adults in maternity roosts is high, the number of lactating females can be estimated by counting the number of nonvolant young in the roost after adults have departed to feed, assuming knowledge of litter size and that all females present in the colony have

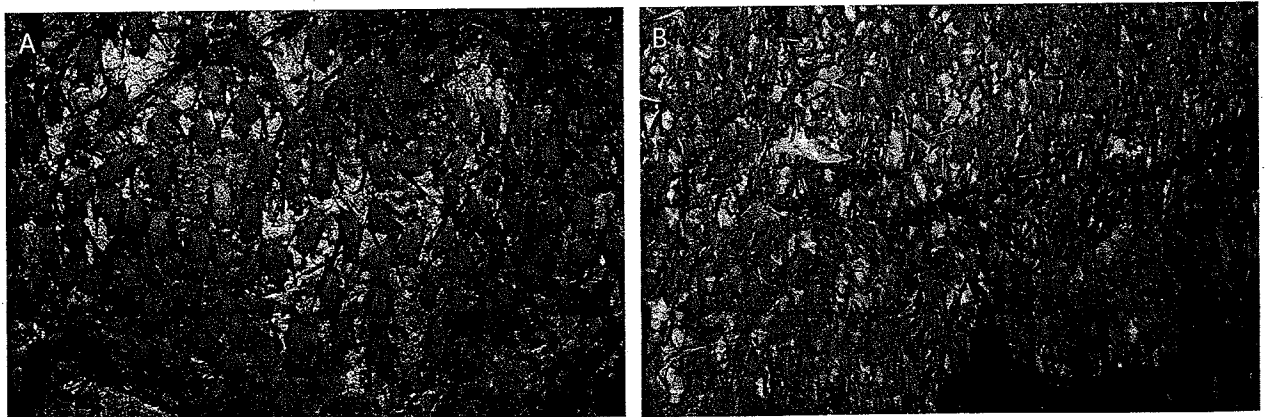


Figure 7.1. Roosting adult Brazilian free-tailed bats (*Tadarida brasiliensis*). A, roosting on the ceiling of a cave in south-central Texas. The numbers of bats present in large cave colonies can be estimated by determining the roosting density of bats at representative sites throughout the cave, calculating an average roosting density, and then extrapolating this average density to the total cave substrate occupied by roosting bats. B, roosting densities of *T. brasiliensis* and other gregarious species often are not uniform. Irregular roost substrates and variable cluster densities of highly gregarious species makes it very difficult to make reliable estimates based on the extrapolation of cluster density to occupied areas of the cave substrate. Photos by T. H. Kunz.

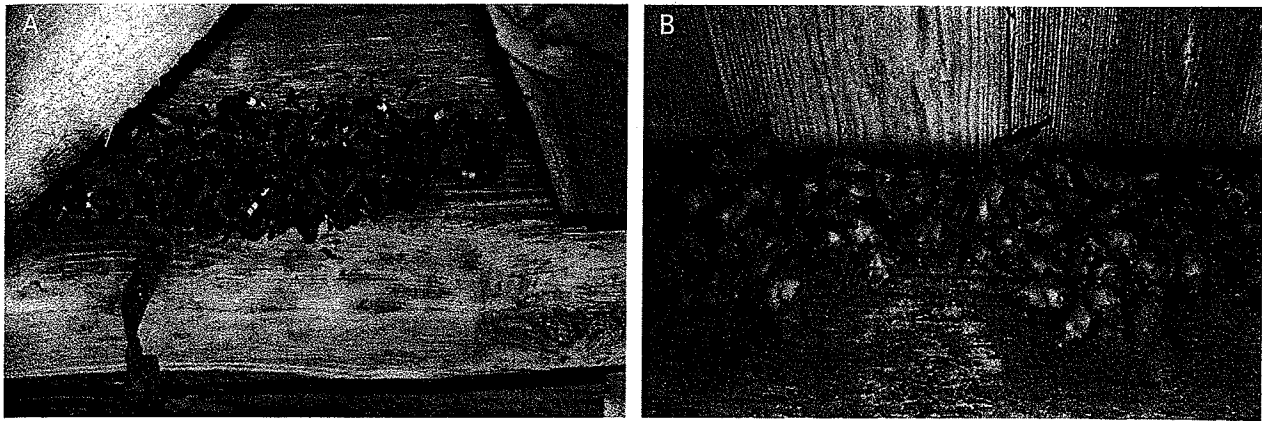


Figure 7.2. Maternity colonies. A, small maternity colony of big brown bats (*Eptesicus fuscus*) roosting near the ridgepole of a barn during late pregnancy; the number of adult bats present in a colony can be censused by direct observation, assuming that all bats are visible. B, young cave myotis (*Myotis velifer*) roosting on the beam of a barn. Photos by T. H. Kunz.

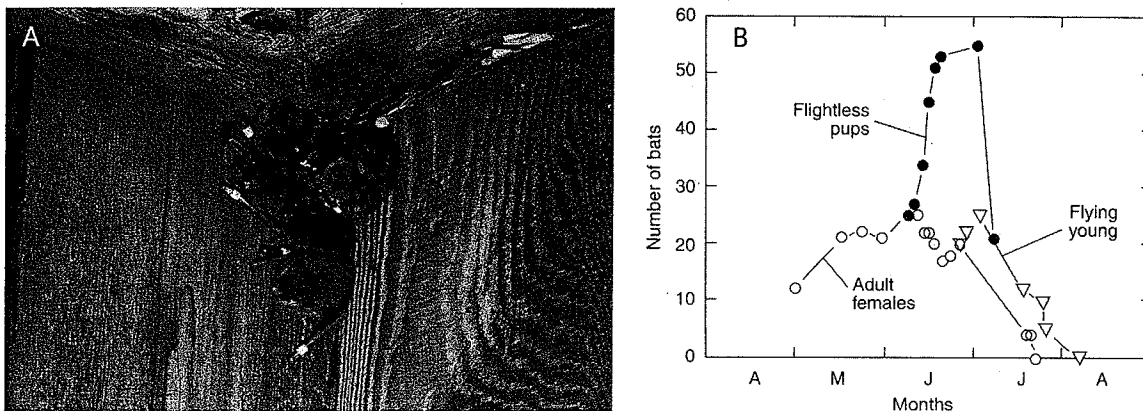


Figure 7.3. Census of a maternity roost. A, small maternity colony of *Perimyotis (Pipistrellus) subflavus* roosting on the ridgepole of a barn; B, census of this colony using multiple methods. Numbers of adult females are based on emergence counts; numbers of nonvolant young observed in the maternity roost following nightly departure of adults; and numbers of volant young estimated from emergence flight counts and individuals observed in roosts. Photo by T. H. Kunz; data from Hoying and Kunz, 1998.

given birth (Figs. 7.2B, 7.3; Kunz, 1974; Tuttle, 1979, 2003; Hoying and Kunz, 1998).

Evening Emergence Counts

Evening emergence counts may be used to census bats that depart from buildings, caves, mines, tree cavities, and rock crevices (e.g., Speakman et al., 1992; Jones and Rydell, 1994; Sabol and Hudson, 1995; Kunz and Anthony, 1996; Hoying and Kunz, 1998; O'Donnell and Sedgely, 1999; Elliott et al., 2006; Betke et al., 2008; Hristov et al., 2008; Hristov et al., in press). In fact, an emergence count may be the only suitable method for censusing bats that roost in physically challenging or inaccessible places (Fig. 7.4). In situations where roosts are unknown, a census may be accomplished by first capturing bats while they

are feeding or commuting, fitting selected individuals with radio transmitters so that they can be tracked back to their roosts (e.g., Kurta et al., 1993; Vonhof, 1996; O'Donnell and Sedgely, 1999; Chaverri et al., 2007). Once a roost has been located in this manner, it may be possible to conduct evening emergence counts.

The number of observers needed to conduct an emergence count will depend on the size and spatial configuration of the roost, number and size of openings from which bats depart, and relative numbers of bats present (e.g., Kunz and Anthony, 1996; Kunz et al., 1996b). Observers should be assigned specific exits or fields of view and should be present at their stations before onset of emergence to ensure that the earliest departing bats are counted.

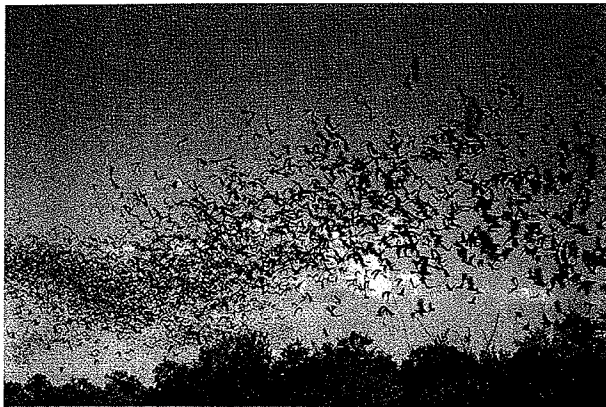


Figure 7.4. Nightly emergence flight of Brazilian free-tailed bats (*Tadarida brasiliensis*) from a cave in south-central Texas. Large colonies such as this one are impossible to census during nightly emergences using direct, unaided observations, especially when nightly emergence extends past nightfall. Photo by T. H. Kunz.

Direct emergence counts of bats are most reliably conducted on species that are locally concentrated, easily observable, and limited in number (Kunz, 2003; McCracken, 2003). Some historic estimates of species that form large colonies, such as Brazilian free-tailed bats (Fig. 7.4), were based on invalid assumptions and technologies and thus are of questionable reliability (Betke et al., 2008; Hristov et al., 2008; Hristov et al., in press). Methods should be standardized and validated so that error estimates can be included. Evening emergence counts of bats also should be made repeatedly throughout the year or season to establish intracolony variation in the number of bats present (Fig. 7.5; Kunz and Anthony, 1996; Hoying and Kunz, 1998; Hristov et al., in press).

Evening emergence counts should be conducted for at least two to three nights during periods of maximum adult colony size (late pregnancy and early lactation) if these data are to be used in comparing peak densities at different sites or between years. To estimate the peak number of adults present in maternity colonies, evening emergence counts should be conducted before young bats become volant. More frequent censusing is advisable if time and personnel are available, and if there is interest in assessing changes in colony size associated with reproductive condition, or the influence of extraneous factors such as changing weather conditions and physical alterations (e.g., gates) or disturbances at roosts. If a census is made after young bats begin to fly, it is important to understand that newly volant young may depart later in the evening than adults (Kunz, 1974; Kunz and Anthony, 1996), thus making it necessary to extend the census period to include these later departures.

Evening Dispersal Counts

Evening dispersal, or "flyout," counts are commonly used to estimate large numbers of megachiropterans that

roost in trees (Thomas and LaVal, 1988; Kunz et al., 1996b; Eby et al., 1999; Garnett et al., 1999; Vardon et al., 2001; Utzurrum et al., 2003; Westcott and McKeown, 2004; Welbergen, 2006). As these bats disperse from their diurnal roosts, it may be possible to count individuals by visually silhouetting them against the sky. However, visibility of bats at the time of nightly dispersal and the experience of observers can greatly influence reliability of estimates using this method. In general, reliability decreases with increasing numbers of bats present, distance of the observer from roost, topography and forest cover, and the ambient light conditions at the time of emergence (Richards, 1990; Kunz et al., 1996a; Utzurrum et al., 2003; Welbergen, 2006). Evening dispersal counts may be underestimated if some individual bats delay departure from the roost until after dark, or observers cannot adequately observe individuals owing to the density of nearby foliage (Kunz et al., 1996a; Utzurrum et al., 2003; Welbergen, 2006). Westcott and McKeown (2004) calculated that roost counts taken by experienced observers during flyouts were, on average, 14.7% lower than counts based on video recordings.

To achieve the most reliable estimates of numbers of bats dispersing nightly from large megachiropteran camps, several observers should be positioned at designated stations at least one-half hour before nightfall. Individuals or teams of individuals should be assigned to count bats as they depart within a pre-assigned arc surrounding the roost. Because decreasing light levels can reduce the visibility of observers, use of light-gathering binoculars or low-light level video cameras may facilitate censusing of dispersing bats in some situations.

Differences in experience among observers in the ability to detect bats dispersing from tree roosts are one of the most serious limitations of this method, thus making it difficult to compare estimates between different investigators (Utzurrum et al., 2003). For example, some bats may not depart from roosts during the twilight period at a time when visual observations are possible. If the probability of detecting individuals or colonies is unknown, the conversion of counts to estimates of abundance cannot be accomplished with any degree of confidence. In some studies, correction factors have been applied to dispersal counts to adjust for different detection rates (Utzurrum et al., 2003) and to account for variation in roost sites (Craig et al., 1994). Future efforts to census such colonies could be improved if assumptions and correction factors were validated (Utzurrum et al., 2003).

Disturbance Counts

Disturbance counts have been used to census some large megachiropteran colonies (Racey, 1979). Typically, this method requires one or more persons to enter a roost area and make loud noises (causing roosting bats to take

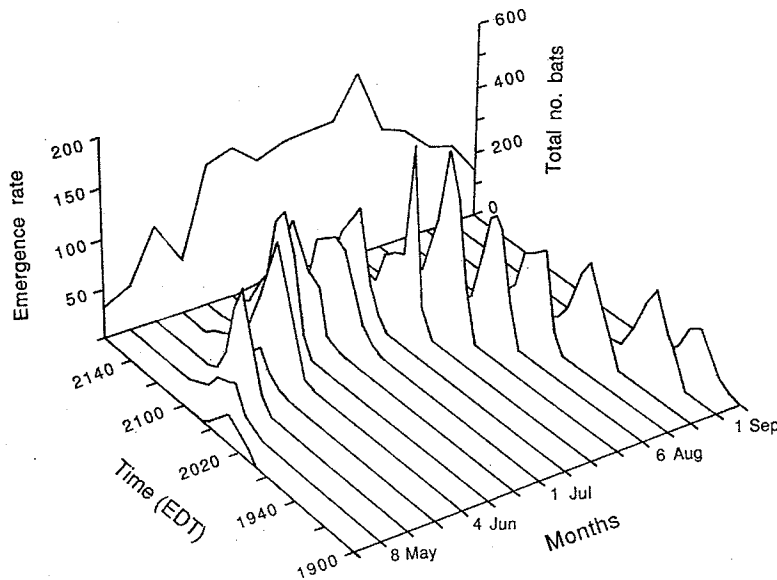


Figure 7.5. Little brown bats (*Myotis lucifugus*) and other species that form relatively small colonies can sometimes be counted as individuals emerge at dusk by silhouetting individuals against a clear sky. Nightly censuses of *M. lucifugus* at a small colony in southern New Hampshire show seasonal trends in numbers present. Seasonal changes in numbers of bats present are indicated on the vertical (y) axis. If bats are counted at 5-min intervals, it is also possible to establish seasonal patterns in nightly emergence. After Kunz and Anthony, 1996.

flight during the day), while other observers count the flying bats. Assuming that all individuals in the colony take flight, individuals may be counted directly, photographed, or videotaped (Dalton and Dalton, 1994). The success of disturbance counts depends on several factors, including sensitivity of bats to planned disturbance, skill of the individuals causing the disturbance, whether all bats simultaneously take flight, and positions of observers relative to the flying bats (Racey, 1979). Because megachiropterans are known to habituate to extraneous noises, the reliability of this method is highly questionable. More importantly, because abandonment of adults and deaths of dependent young have been observed following such disturbances (Garnett et al., 1999), continued use of this method should be approached with caution.

Advanced Censusing Methods

Reflectance Infrared Imaging

Night vision goggles (NVGs), night vision scopes, and near infrared cameras are increasingly used to observe and census bats as they emerge nightly from caves, mines, buildings, and tree cavities (Elliott et al., 2006). These devices have proven valuable in situations where ambient light is limited and a supplemental light source is required, typically in the long-wave infrared bandwidth to which the electronics are most sensitive. These devices also are sensitive to visible spectrum, but because bats also are highly sensitive to visible light, infrared illumination should be

used to avoid or minimize disturbance while censusing bats that emerge after sunset.

Tripod-mounted night viewing devices, cameras with supplemental light sources, or thermal infrared cameras should be positioned so that emerging bats fly perpendicular to the field of view. Night vision goggles and scopes offer an advantage to the researcher in being able to view emergences of bats after nightfall, although manual counting of bats is generally necessary at the time of the actual emergence unless the device is coupled to a video camera and the images are recorded on videotape (Dalton and Dalton, 1994; Fleming et al., 2003). Digital video cameras sensitive to the infrared spectrum (e.g., Sony Night-Shot) offer many advantages over NVGs and scopes because they can capture a permanent record that can be analyzed later, either manually or using computer algorithms for automatic detection and counting (Elliott et al., 2006). Cameras with the highest available frame rates provide the best images for analysis (see Altenbach and Dalton, this volume).

Thermal Infrared Imaging

Thermal infrared imaging offers an important advantage when censusing bats during nightly emergences because individual bats can be detected and counted independent of ambient (visible) light. As with near infrared cameras, thermal infrared cameras should be positioned so that emerging bats fly perpendicular to the field of view

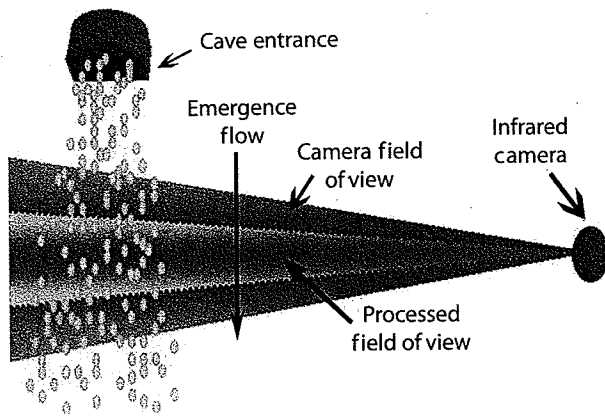


Figure 7.6. Schematic diagram depicting the camera position and field of view of a thermal infrared camera used to census large numbers of bats as they emerge nightly from a cave roost. After Kunz, 2004.

(Fig. 7.6). Use of thermal infrared cameras when coupled to computers offer considerable promise for censusing colonies ranging from a few hundred to several million individuals (Sabol and Hudson, 1995; Frank et al., 2003; Betke et al., 2008; Hristov et al., 2008; Hristov et al., in press). Using this method, Sabol and Hudson (1995) counted 47,000 gray bats (*Myotis grisescens*) that emerged from a cave in Alabama, and Frank et al. (2003) estimated that 1.5 million Brazilian free-tailed bats emerged from a cave in south-central Texas.

The analytical methods associated with thermal infrared imaging used by Sabol and Hudson (1995) and Frank et al. (2003) identified bats as they appeared in a given frame and then subtracted the thermal images of bats from a background frame that did not contain bats. In these two studies, estimates were made by dividing the number of detected bats (summed throughout the emergence period) by one or more estimates of flow rate (determined by counting the number of frames in which a single bat appeared). More recent analyses, using computer vision algorithms (Betke et al., 2008; Hristov et al., 2008; Hristov et al., in press), have shown that flow rates are highly variable and thus should be factored into the analysis to accurately and reliably estimate colony size.

Recently, computer vision algorithms have been developed to automatically detect and track emerging bats, without the need to correct for variable flow rates (Betke et al., 2007; Betke et al., 2008; Hristov et al., 2008; Hristov et al., in press). The detection algorithm is based on an image filter that automatically distinguishes warm regions of bats (typically the body) from the vegetation, clouds, and other objects in the background (Fig. 7.7). A filter computes threshold values that are automatically adjusted to the current temporal and spatial characteristics of the image. For example, comparing a pixel's current value with its range of recently measured values makes it possible to identify pixels representing sky and vegetation and

remove them from further analysis. A local intensity peak in the original frame that is contained in some region of the filtered frame corresponds to the warmest visible part of a bat's body—typically its thorax. The numbers of these peaks are used to estimate the number of bats present in a video frame.

Two image filters are used to detect image regions that include bats or other flying organisms (birds and sometimes large insects). The first filter uses frame differencing to eliminate pixels with small intensity changes from frame to frame. The second filter automatically computes thermal threshold values that are adjusted to current spatial and temporal characteristics of the image. To characterize the range of intensities observed at a given pixel over a number of frames, the sample mean and standard deviation of the pixel's intensity values are computed over these frames.

After filtering, each frame is processed to identify regions of the remaining pixels immediately adjacent to one another. Region size depends on the bats' distance from the camera, the positions of their wings, and whether one or more bats have partially occluded others. High intensity values in these regions correspond to warm parts of the bats (thoraxes), whereas lower intensity values correspond to cooler parts (e.g., wing membranes).

To estimate the number of bats, the number of local intensity peaks in the original frame is used. With this method, it is possible to accurately quantify the number of bats in images where the apparent size of some bats is so large that the number of local intensity maxima cannot serve as a reliable estimate of the numbers present in a region of interest. In most emergence images, bats appear as small collections of pixels. Numbers of bats derived from this method are as reliable as estimates made by a human observer watching the video output (Fig. 7.8).

As with most other methods, counting bats with thermal infrared cameras can be challenging, owing in part to irregular topography at the site, adverse weather conditions (e.g., rain or wind), limited field of view, as well as variability in the pathways of emerging bats relative to the fixed position of a camera. It is sometimes difficult to position a camera so that all emerging bats appear in its field of view throughout the entire emergence period, because a column of emerging bats may shift direction or spread out over larger areas than can be detected in the camera's field of view. Moving a camera during the sequence of emergence videos creates technical difficulties in post-recording analyses.

Currently, we use FLIR/Indigo Systems Merlin Mid infrared thermal cameras (FLIR, Billerica, Massachusetts, www.flirthermography.com) to capture 12-bit intensity values in 320×240 digital video format ranging from 30 to 60 frames per second directly onto the hard drive of a computer. Depending on the size of the emergence col-

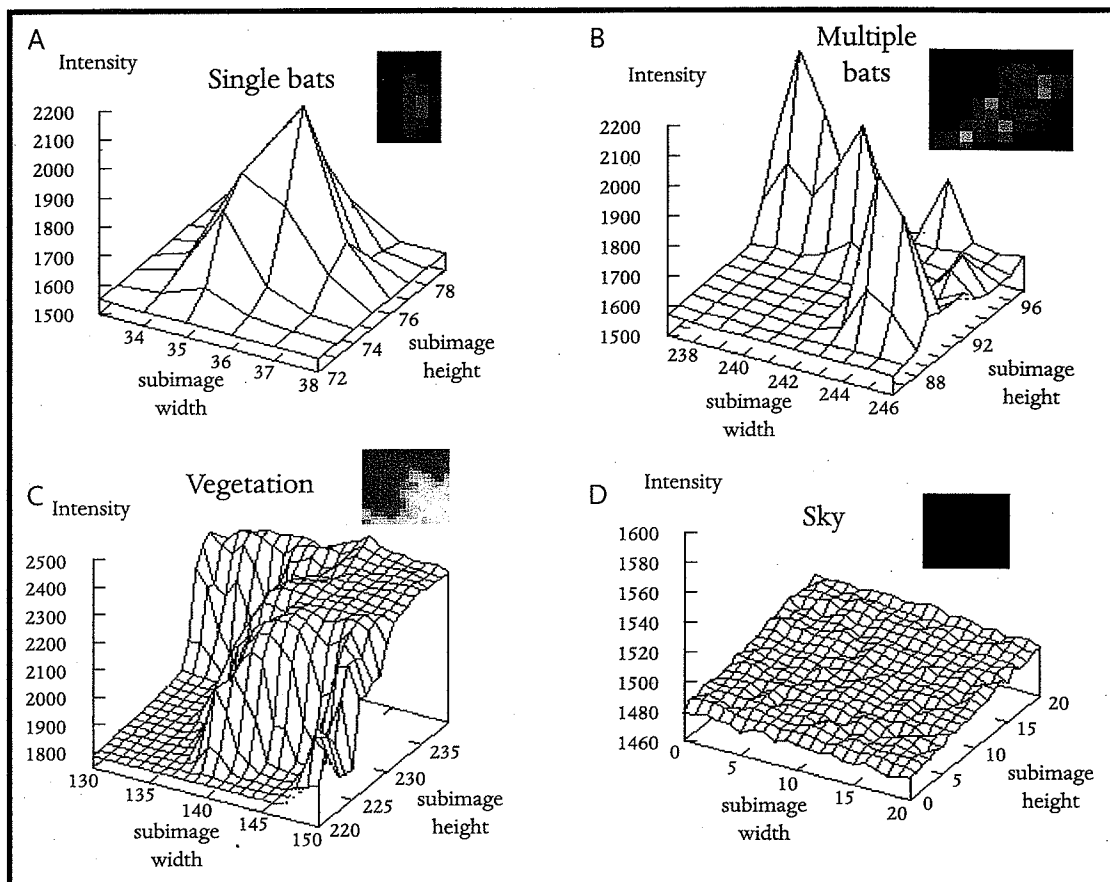


Figure 7.7. Thermal infrared images and three-dimensional computer vision depictions of single and multiple bats (A and B), vegetation (C), and sky (D). After Betke et al., 2008.

umn, we use either 13- or 25-degree lenses that allow us to record most of the emerging bats, although the apparent images of some bats viewed with a 13-degree lens may be too small and difficult to detect. It is especially difficult to distinguish individual bats from warm backgrounds that contain solar-heated vegetation and clouds. At present, the principal limitation of thermal infrared cameras for censusing bats is the relatively high purchase U. S. price (\$60,000–\$100,000). Newer models with higher frame rates are becoming increasingly available at lower cost, and leasing such cameras may be preferable to purchase for some field applications.

Capture Mark Recapture

Capture-mark-recapture methods can be used successfully to estimate abundance of bats only if certain assumptions are met (O'Shea et al., 2004). A major assumption of this method is that the population or colony being censused is "closed." A colony of adults is considered closed only during a brief period in late pregnancy and early lactation when females exhibit the strongest fidelity to their roosts, before young become volant, and adults begin to emigrate. In principal, a population is considered closed

when recruitment, mortality, emigration, or immigration are non-existent during the census period (Nichols and Dickman, 1996). Some recent models have relaxed the latter assumption, but other assumptions raise questions about the validity of this technique when applied to most bat species. Among these assumptions are that (1) no differences in mortality exist between marked and unmarked animals, (2) marked and unmarked individuals have the same probability of being recaptured, (3) marks are not lost or overlooked, and (4) marked animals mix freely and randomly within the study population.

Unbiased capture methods and suitable marking methods are essential for successful mark-recapture studies. Many species require different capture and marking methods (Barclay and Bell, 1988; Kunz and Kurta, 1988; Kunz, 1996; Kunz et al., 1996a, Kunz and Weise, this volume). Some species fail to tolerate traditional marking methods, and others cannot be captured repeatedly without causing unacceptable disturbance to colonies. Use of PIT (passive integrated transponders) tags for marking bats holds considerable promise for mark-recapture studies because the marks generally persist, and the presence of marked individuals can be readily detected with PIT tag readers or

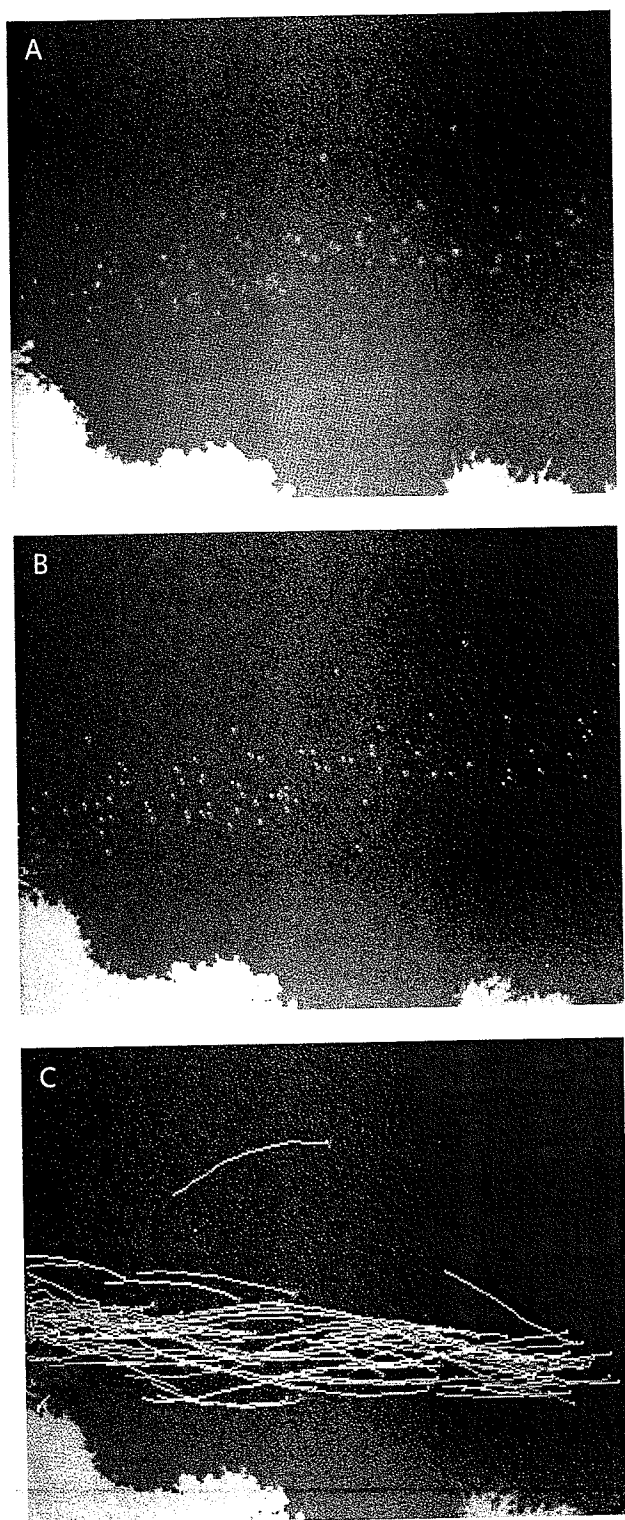


Figure 7.8. Thermal infrared imaging using computer vision algorithms. A, Brazilian free-tailed bats emerging from a cave in south-central Texas; B, images of the same emerging bats to which an object detection algorithm was applied; C, images of the same bats to which an automatic tracking algorithm was applied and used for censusing. Photos by T. H. Kunz, N. I. Hristov, and M. Betke.

loop antennae (Kunz and Weise, this volume; O'Shea et al., 2004).

To date, PIT tagging has been used successfully in a handful of studies on bats with minimal injury or loss of tags (Kerth and König, 1996, 1999; Brooke, 1997; Horn, 1998; Kerth and Reckardt, 2003; O'Shea et al., 2004). Once animals are marked, potential biases associated with recapture, such as trap happiness or trap shyness, can be ignored. Mark-recapture studies of bats that use PIT tags, however, do not obviate the need to satisfy other assumptions (O'Shea et al., 2004). Available software programs such as CAPTURE (Otis et al., 1978) and MARK (White and Burnham, 1999) take into consideration differences in behavior among individuals, temporal variation in capture probabilities, and initial capture and subsequent recapture probabilities. A detailed review of mark-recapture methods is beyond the scope of this chapter. However, relevant evaluations and discussions of various mark-recapture techniques and models can be found in White et al. (1982) and Thompson et al. (1998). For reviews and discussions of published mark-recapture studies on bats, the reader is referred to Thomas and LaVal (1988), O'Shea et al. (2004), and O'Donnell (this volume).

Estimates of Colony Size Based on DNA Markers

Molecular markers also may be used to provide information on population structure and demographic trends within populations. For example, when direct captures are difficult or undesirable, capture-mark-recapture models have been used to estimate population sizes based on noninvasive genetic samples of feces or hair. Using this approach, Puechmaille and Petit (2007) compared estimates of colony sizes of the lesser horseshoe bat (*Rhinolophus hipposideros*) based on DNA extracted from feces, with independent estimates derived from visual counts conducted during nightly emergence. Their results suggest that DNA extracted from feces can be used to accurately estimate colony size. Similar non-invasive approaches using skin and hair may be useful for estimating the abundance of bat species that are otherwise challenging to census directly.

As with traditional demographic methods, the reliability of population estimates based on molecular methods is influenced by certain assumptions. For example, colony size can be under- or overestimated if scoring errors are made when the alleles of heterozygous individuals are not amplified during a positive PCR (polymerase chain reaction), or when PCR-generated alleles create a slippage artifact during the first cycles of the reaction (Waits and Leberg, 2000; Waits, 2004). Errors of this type can be corrected by repeating the process of genotyping and comparing genotypes to each other (Paetkau, 2003).

SPECIAL CHALLENGES OF CENSUSING BATS

Hibernating Species

Census efforts directed toward hibernating bats should be designed to reduce disturbance and to minimize the incidence of arousals. Ideally, a hibernating colony should not be censused more often than once every two years (Kunz, 2003). Species that roost in small, discrete clusters can be counted individually as they are encountered (Fig. 7.9A). For species that form large aggregations (Fig. 7.9B), colony size is best determined by estimating the cluster density at selected sites, and then extrapolating this value to the total area of the roost substrate covered by the bats (Tuttle, 1979, 2003). Species identifications based on visual assessment rather than handling are preferred in order to reduce disturbance. Personnel engaged in censusing hibernating bats should not only be familiar with species identification, but should also have experience with caving techniques and knowledge of appropriate human safety and rescue procedures. The size and complexity of the hibernaculum (e.g., number and size of chambers and rooms, number of levels, and overall access) will dictate the number of individuals necessary to conduct a thorough census of bats present in caves and mines. Census teams should make every effort to minimize the amount of time conducting a census to reduce disturbance to bats.

Foliage- and Cavity-roosting Species

Direct visual counts of some gregarious, foliage-roosting megachiropterans may be possible in situations where the colonies are relatively small and/or where roost trees have been fully or partially defoliated, making it possible to see all or most of the roosting bats present (Fig. 7.10A). Because colonies of many gregarious species are large and diffuse or obscured by surrounding vegetation (Fig. 7.10B), a roost census may only yield estimates in or-

ders of magnitude. In very large colonies of pteropodids, for example, incremental counts (e.g., 1–100; 100–1,000; 1,000–10,000; and over 10,000) have been used for extrapolating to larger areas occupied by the colony (Vardon and Tidemann, 1997, 1999). If numbers of roosting bats cannot be assessed reliably, nightly dispersal counts may prove useful (Kunz et al., 1996b).

Methods for censusing solitary, and often cryptic, foliage-roosting mega- and microchiropterans (Fig. 7.11A) have largely been limited to random searches or have been confined to areas where investigators have previously established transects or developed search images of foliage that has been modified into tents (e.g., Storz et al., 2000; Hodgkison et al., 2003; Campbell et al., 2006; Chaverri and Kunz, 2006). Other methods are based on systematic surveys of particular roost types, such as furled leaves (Vonhof and Fenton, 2004) or tree cavities (e.g., Lumsden et al., 2002a; Clark, 2003; Barclay and Kurta, 2007).

Radiotelemetry also has proven useful for locating small bats that roost in foliage (Fig. 7.11B), tree cavities, rock crevices, and beneath bridges (e.g., Barclay et al., 1988; Kurta et al., 1993; Barclay and Brigham, 1996; Betts, 1996; Kalcounis and Hecker, 1996; Sasse and Pekins, 1996; Vonhof, 1996; Menzel et al., 1998; O'Donnell, 2000; Bogan et al., 2003; Carter et al., 2003; Clark, 2003; Chaverri and Kunz, 2006; Arnett, 2007; Amelon et al., this volume). Once such roost sites are located, censusing based on emergence counts facilitated by binoculars, night vision devices, or thermal imaging cameras has proven useful. In addition to or complementary with the use of radiotelemetry for locating roosts, other methods—such as grids, transects, and defined areas—should also be considered when assessing abundance. No matter what methods are used to assess the abundance of foliage-roosting, tree-cavity roosting, and crevice-dwelling bats, the census should be designed to reduce sample biases and to minimize disturbance.

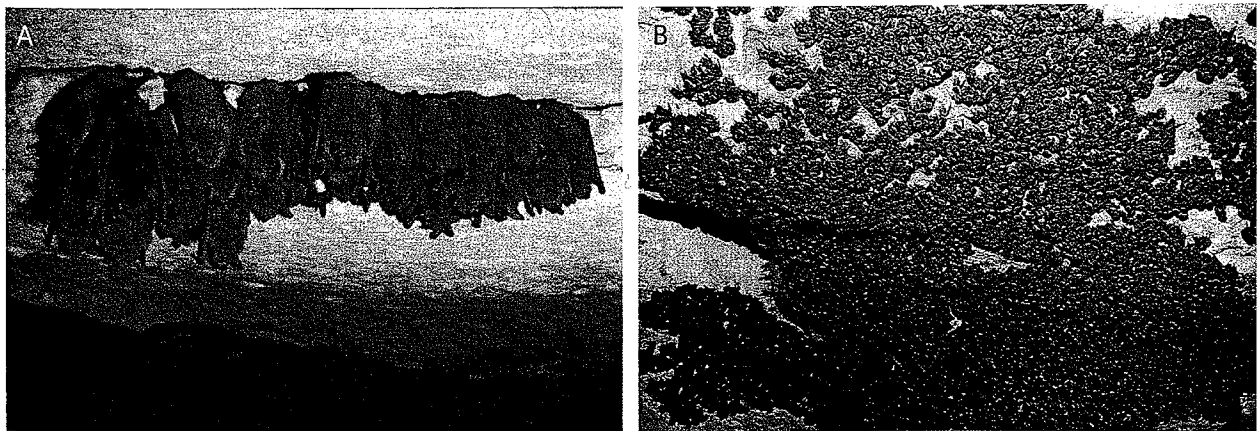


Figure 7.9. Bats in hibernating clusters. A, small cluster of cave myotis (*Myotis velifer*); B, large clusters of gray bats (*M. grisescens*). Photo A by T. H. Kunz; photo B by M. D. Tuttle.

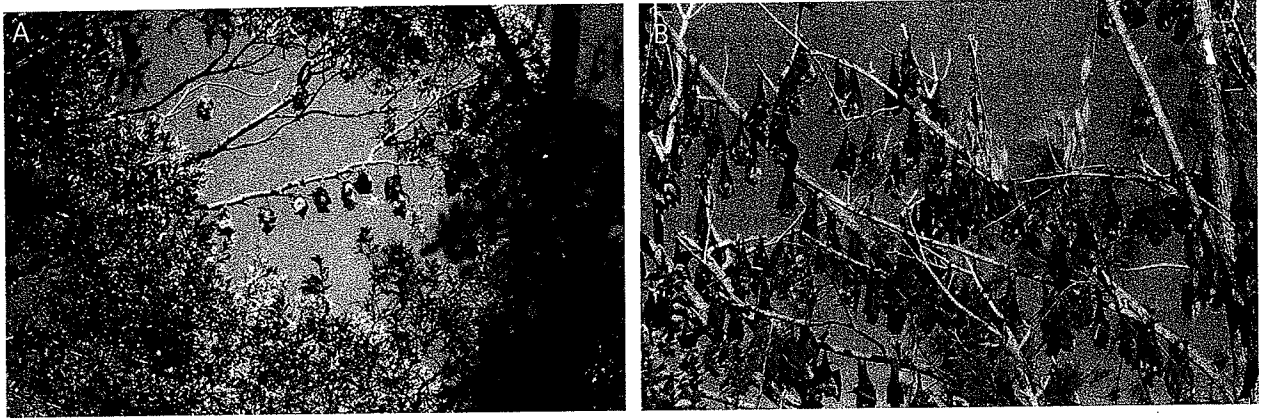


Figure 7.10. Foliage-roosting bats. A, a colony of giant flying foxes (*Pteropus giganteus*) roosting in a partly defoliated tree near Pune, India, may be censused from ground level, assuming that all bats can be observed; B colony of gray-headed flying foxes (*P. poliocephalus*), roosting in the crown of a somewhat densely foliated tree in eastern Australia. Dense foliage and sensitivity of bats to presence of observers may preclude direct censusing from ground level. Photo A by T. H. Kunz; photo B from Hall and Richards, 2000.

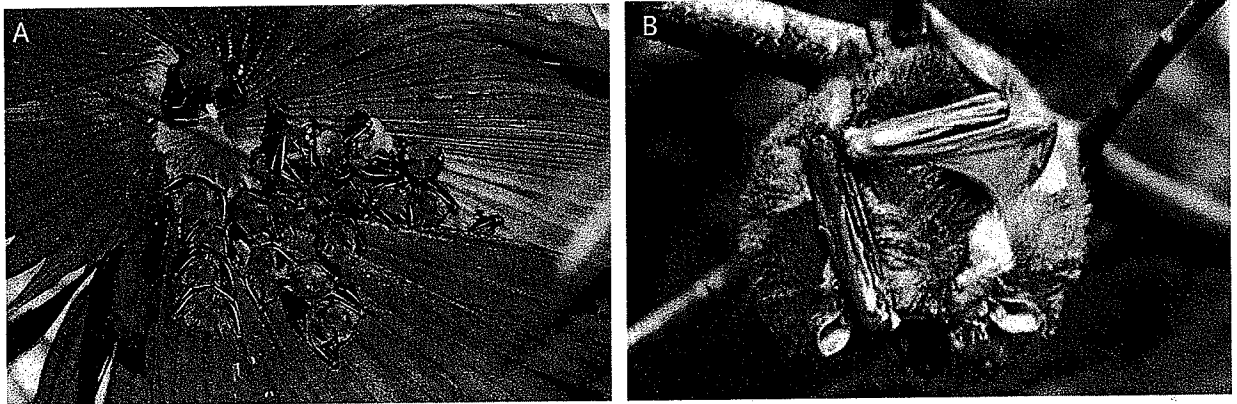


Figure 7.11. Small foliage-roosting bats. A, harem group of short-nosed fruit bats (*Cynopterus brachyotis*) roosting beneath a palm leaf that was modified into a tent; B, small family group of red bats (*Lasiurus borealis*) roosting in the understory of a deciduous tree. Some foliage roosting bats can be observed and counted directly, although roost locations usually must first be located using radiotelemetry, by intensive visual searches (based on established search images of roosts), or by listening to echolocation calls. Photos by T. H. Kunz.

Censusing Bats in Buildings

Efforts to census bats that roost in buildings pose other challenges. For example, some property owners do not permit researchers to enter their homes and other buildings for the purpose of censusing bats; and even if access is allowed, many bats occupy crevices and cavities that cannot be observed and counted directly. Evening emergence counts provide the most reliable estimates and generally are most successful when colonies are relatively small (fewer than 1,000 individuals; Kunz et al., 1996b; Hoying and Kunz, 1998). Depending on the number of observers, it may be possible to count all or most of the bats that emerge from buildings at dusk by silhouetting them against the sky at dusk (Kunz et al., 1996b; Hoying and Kunz, 1998; Kunz and Reynolds, 2003), or by recording (and counting) them using reflectance infrared video

(Frantz, 1989) or thermal infrared cameras (Hristov et al., in press). Notwithstanding, colony censuses based on nightly emergence counts can be biased when bats regularly shift to alternate roosts (Brigham and Fenton, 1986; Lewis, 1995; Barclay and Brigham, 1996). Roost-shifting behavior by species that form fission-fusion colonies highlights the need for researchers to explore all possible exit routes and nearby alternate roosts before conducting a colony census (Thomas and LaVal, 1988; Kunz et al., 1996b).

ESTIMATING EFFECTIVE POPULATION SIZE

Patterns of genetic variation may be used to estimate effective population size (N_e) and population trends (growth or decline). From an evolutionary perspective,

the effective population size, N_e , is a critical parameter, as it directly reflects the rate at which a population will lose genetic variation through stochastic processes such as genetic drift (the rate of loss of variation is negatively correlated with N_e). As such, estimates of N_e are important for assessing the status of and managing endangered and threatened species, and for understanding how populations may respond to natural and anthropogenic perturbations, such as habitat loss, degradation and fragmentation, or climate change.

Several approaches using molecular markers are available to estimate N_e and to assess changes in population size over both short and long time-scales. A complete discussion of these methods is beyond the scope of this chapter, and thus we refer readers to Beebe and Rowe (2004), Lowe et al. (2004), and Freeland (2005) for general reviews, and to Luikart et al. (1998), Avise (2000), Spencer et al. (2000), Leberg (2005), and Wang (2005) for more detailed methodologies. Here we briefly outline some of the most widely used and powerful methods to illustrate the general approaches.

Short-term N_e can be estimated by sampling a population at one point, sampling it again some number of generations later, and then estimating allele frequencies at each sampling period. The change in genetic variation between the sampling periods due to drift is directly proportional to N_e , assuming that no other factors (selection, migration, or population structure) are influencing the population. Assessing temporal changes in allele frequency requires the use of highly variable markers (i.e., microsatellites), and the sample size, number of markers, and number of generations between sampling periods influence the accuracy of the estimate. The estimate obtained is the N_e during the period over which the samples were taken.

Temporal variation in allele frequencies also can be used to infer population bottlenecks, for the same reasons as outlined above (Luikart et al., 1998). Other methods may be used to detect population bottlenecks, including changes in allelic diversity, which declines directly with population size (Leberg, 1992). Similarly, during a population bottleneck, the number of rare alleles will decline more rapidly than heterozygosity, leading to a temporary excess of heterozygotes in the population relative to a population at equilibrium. Using data on allele frequencies, it is possible to test for a significant excess of heterozygosity within a population due to a bottleneck (Cornuet and Luikart, 1996). Because only a single sample is required, this method may be more widely applicable than other methods, but it requires the genotyping of a large number of polymorphic loci and may only be sensitive to very recent, severe bottlenecks (Spencer et al., 2000).

Long-term N_e is often estimated using a coalescent approach, which we briefly introduce here. The genetic variation at any particular gene in a population can be illus-

trated as a topology ("gene tree") reflecting the historical relationships or genealogy of the gene copies found in different individuals. The number of mutations (i.e., nucleotide substitutions) separating these variable DNA sequences is a function of the demographic history of the population. Because mutations accumulate through time, sequences that diverged longer ago will be separated by a larger number of mutations than those that diverged more recently. If a historically large population remains large, its gene trees will have many "branches" of varying lengths that reflect the accumulation and retention of both older and younger mutations. If a large population is reduced in size, its gene tree will be "pruned." That is, genes reflecting both long and short branches will be lost with the result of less overall diversity. However, short branches will be proportionately fewer in the reduced population because fewer recent mutations occur and they are less likely to be retained, simply because of the reduction in population size. Correspondingly, if a population that was historically small expands in size, new lineages are more likely to survive than in a constant population, and thus the gene tree will consist mostly of short branches reflecting increased occurrence and retention of more recent mutations.

Coalescent theory is a retrospective model of population genetics that traces the historical divergence and extinction of alleles of a gene in a population backward through time to a single ancestral copy (i.e., the point at which they coalesce), and interprets the distribution of times to common ancestry in a gene tree in terms of various evolutionary forces, including genetic drift, migration, population size changes, and selection. It essentially makes use of the pattern of coalescent events to estimate a wide range of important population parameters, such as N_e , the population growth rate (either increasing or decreasing), population divergence times, migration, mutation, and recombination rates (Rosenberg and Nordborg, 2007).

Modern coalescent methods allow researchers to simultaneously estimate multiple parameters, including long term N_e and population growth rate. The coalescent approach only requires the sampling of a population once (although information can be gained from multiple, temporally spaced samples), and then coalescent simulations can be used to identify the most likely genealogy and associated parameters given the current patterns of genetic variation. Coalescent methods typically rely on DNA sequence data but may also incorporate other types of markers (such as microsatellites); generally, confidence in estimates increases with the number of independent markers employed. The estimates of N_e or growth rate obtained using the coalescent approach are typically long-term averages over evolutionary time, the time scale of which is determined by the specific marker(s) used in the study. However, models that simultaneously estimate these parameters can provide current estimates of N_e .

Beyond its direct applicability to the management of genetic variation in small populations, the estimation of N_e is also valuable for assessing population trends. By comparing temporally spaced estimates of short-term N_e , or short- and long-term estimates of N_e , it may be possible to detect population trends over time. For example, the historical population sizes of humpback and fin whales prior to hunting by humans were estimated to consist of approximately 240,000 and 360,000 whales, respectively, contrasted to modern population sizes of 10,000 and 56,000 individuals (Roman and Palumbi, 2003). Historical estimates of effective population size of grey wolves prior to human settlement of North America was estimated at approximately 5,000,000, as compared to the current estimate of 173,000 (Vilà et al., 1999).

For bats, coalescent analysis suggests an expansion of migratory populations of Brazilian free-tailed bats approximately 3,000 years ago, a date that corresponds with the occurrence of a wetter climate and increased insect availability (Russell et al., 2005; Russell and McCracken, 2006). This was apparently followed by an approximately 16-fold decline in estimated population size in more recent times (Russell et al., 2005; Russell and McCracken, 2006), perhaps as a consequence of human activity.

From the perspective of the conservation and management of bats, it is important to know whether the species of interest exists in a single, panmictic population or in a series of discrete subpopulations that may or may not be connected by migration (gene flow) and that may be experiencing independent demographic trends. Molecular markers can be used to examine levels of population differentiation within a species and to delineate populations or groups of populations based on the observed distribution of genetic variation. Importantly, such analyses can be used to define the relevant unit for population monitoring and highlight demographic connections among populations that may not be obvious from behavioral data alone. Population genetic studies on a number of bat species show high levels of genetic diversity and little population-level structuring (e.g., Ditchfield, 2000; Russell and McCracken, 2006), whereas other species show relatively low levels of genetic diversity and high levels of population structure (e.g., Wilkinson and Fleming, 1996; Campbell et al., 2006b; Weyandt et al., 2007). Thus, the geographic extent and size of populations may differ dramatically among species. The implications of these and other studies using molecular markers (Avise, 1992, 2004) indicate that different species are subject to different risks from anthropogenic drivers, and should be studied to assess whether a given species is more or less at risk from changing environments. Collecting wing biopsies and analyzing DNA from bat tissue can be a valuable approach for assessing genetic variation, population structure, and N_e . Ideally, tissue for genetic analyses should be collected

for all species captured or discovered at a given location. When necessary, representative specimens and especially unidentifiable carcasses (e.g., killed at wind turbines) should be collected in their entirety and deposited as voucher specimens in museums. Use of mitochondrial and nuclear DNA sequence data derived from hair and skin of carcasses also offers the potential for identifying closely related or cryptic species (e.g., Barratt et al., 1997; Mayer and von Helversen, 2001).

ABUNDANCE INDICES

At times, it may be necessary to use indices of abundance to convey information about a colony or population. Ideally, an abundance index should vary in some manner that is proportional to actual abundance (Caughley, 1977). A researcher may choose to use an abundance index rather than a more direct measure (e.g., direct count or statistical estimation) of a colony or population for several reasons. For example, individuals of some species may be difficult to observe or capture because of their cryptic roosting habits, social structure, or inaccessibility to roosts (O'Shea et al., 2004). Moreover, an abundance index may be more cost effective and less time consuming than conducting a direct count or statistical estimate (Conroy, 1996).

Owing to difficulties often inherent in censusing bat populations, survey and monitoring programs commonly rely on indices of abundance to infer patterns of abundance. A colony or population index is a statistic assumed to be correlated with the true parameter of interest (Thompson et al., 1998). In general, a colony or population index is an incomplete count of individuals that is assumed to be proportional to the true abundance (Conroy, 1996). For example, a frequently used colony or population index of abundance is "catch per unit of effort," expressed as number of bats captured per night, per net-hour, or net-meters per night (Kunz et al., 1996a; Hayes et al., this volume; Kunz, Hodgkison, and Weise, this volume).

That colony or population indices of abundance based on captures are proportional to true abundance is an assumption that is rarely, if ever, tested. This means that an index of abundance may be unreliable. For example, differences in capture or detection probability may differ among sites or times due to variation in amounts of time spent foraging in a given habitat, reproductive activity, weather conditions, or capture efficiency (Hayes et al., this volume; Kunz, Hodgkison, and Weise, this volume). Because capture probabilities can differ with respect to time, species, sex, reproductive status, capture method, and habitat, the value of abundance indices based on capture data is dubious at best (Remsen and Good, 1996; O'Shea and Bogan, 2003; Vonhof and Fenton, 2004). In monitoring programs that use mist nets or harp traps,

capture probabilities may vary considerably among nights or locations, sex and age of individuals present, and thus may only provide a crude estimate of abundance when using such indices.

The relationship between an abundance index and actual abundance may be linear or non-linear. Abundance indices often have non-linear relationships with true abundance. For example, a colony index of abundance may be influenced by behavior that changes in a density-dependent manner. For example, if subordinate males in a social group of *Phyllostomus hastatus* or *Artibeus jamaicensis* join a harem group more frequently at high densities than at low densities (Kunz et al., 1998; Ortega and Arita, 2002), then estimates of abundance could be confounded by density dependent effects.

Direct Indices of Abundance Based on Capture and Observations

Abundance indices may be direct or indirect (Conroy, 1996). Direct indices are based on direct observations, either visual or by capture. An incomplete count is one form of a direct index in which animals are counted, but the count does not include every individual present because some animals may be overlooked or missed. Incomplete counts can be based on surveys of roosting bats or aerial surveys of foraging bats. As with other direct indices, n animals are observed in a sample and these individuals constitute some unknown proportion of the total population. When an index is proportional to the actual population, the direct index is $n = b_1 N$, where the proportionality constant b_1 represents an observed fraction.

Incomplete counts may result from missing some animals or counting others more than once. For example, individuals of some bat species may reenter roosts during nightly emergence counts (e.g., Thomas and LaVal, 1988; Kunz and Anthony, 1996), and thus should be accounted for. If multiple counting of individual bats occurs with sufficient frequency, then the slope of the constant b_1 relating the index to actual abundance will be less than one. To our knowledge, no efforts have been made to validate relationships between incomplete counts and true abundance in colonies or populations of bats.

An abundance index based on the number of individuals captured per unit time and effort (e.g., trap or mist-net effort) is known as a capture index. An implicit assumption of capture indices is that changes in captures over time represent proportional changes in abundance (Conroy, 1996). Capture probabilities can vary both within and among species, between sexes, age, reproductive condition, and habitat. Moreover, because there is considerable evidence of species-specific differences in foraging height (e.g., Kalko and Handley, 2001; Hodgkison et al., 2004; Rex et al., 2008), capture indices may be biased based on where capture devices are positioned. Moreover, some

species have different abilities to detect nets, and thus may be regarded as being "net happy" or "net shy."

Surveys of the number of occupied roosts in designated areas (e.g., number of caves, buildings, tree cavities, leaf tents, rock crevices), without direct counts of the number of individuals within them, provide little information for developing indices of population abundance. Only when numbers of available roosts are combined with estimates of numbers of occupied roosts can estimates of populations be determined. However, finding all possible roosts in a defined area may be exceedingly difficult. Within confined roosts such as caves and tree cavities, some unknown proportion of a colony may be missed or overlooked during direct counts (Thomas and LaVal, 1988). For example, when sampling harem groups during the mating season, dominant males often resist capture efforts, whereas females and their dependent young are more vulnerable to being captured (e.g., Kunz et al., 1983; Storz et al., 2000; Ortega and Arita, 2002; Chaverri and Kunz, 2006).

Indirect Indices of Abundance Based on "Sign"

Indirect indices of abundance are based on evidence of an animal's presence (e.g., guano volume and distribution, acoustic surveys, and roost surveys), but not on observations or captures of animals. Indirect abundance indices are based on the assumption that when animals are absent the index value is zero, and subsequently increases with increased levels of true abundance. Ideally, indirect indices should be linear, although monotonic relationships also have been reported (Conroy, 1996).

Both contemporary and historical estimates of deposits of guano have been used as indirect abundance indices for bats (Tuttle, 1979, 2003). The critical assumption in using this approach is a constant and consistent relationship between amount and distribution of guano on the floor of a roost site and the abundance of bats (Constantine, 1967; Tuttle, 1979). However, this assumption has not been evaluated owing to the absence of robust data about the relationship between defecation rates, and daily or seasonal use of roosts by bats.

Because guano deposition in roosts can be ephemeral, and subject to change within and among roosts, using such deposits is of limited use for estimating abundance of bats. Other complications with measuring guano deposition include the influence of organisms (e.g., insects, fungi, and bacteria) that use this substrate as a nutrient, as well as changes in humidity, temperature, and water flow. Before guano deposition can be used as an index of relative abundance, one would first need to establish baseline data on rates of deposition, identity of species producing the guano, and rates of degradation by each species (Hayes et al., this volume). Currently, the identity of species that

produce guano can be determined by species-specific DNA signatures (Zinck et al., 2004).

As with the accumulation of guano, staining of roost substrates by bats can vary according to species; physical characteristics of the cave, mine, or building (Thomas and LaVal, 1988; Tuttle, 2003); and uncertainties about the identity of species that produced the stains. Thus, use of stain on roost substrates can be a misleading variable when trying to assess the relative abundance of bats or a given species of bat. In our judgment, the use of stains on roost substrates to estimate relative abundance of bats will remain dubious until such time it can be validated using independent methods.

Indirect Indices of Population Abundance Based on Roost Surveys

Surveys of the number of occupied roosts (e.g., cave, buildings, bridges, tree cavities, leaf tents, rock crevices), without direct counts of the number of individuals within them, can provide some information for developing indices of abundance. These and similar structures should be surveyed based on predetermined designs, such as stratified random plots or systematic quadrats, or computed for a given sample area (e.g., number of tree cavities per hectare). Uses of such indices assume that they are proportional to the number of animals present in the study area (Chaverri et al., 2007). A key assumption of indirect population indices is that the number of animals per roost structure is the same between surveys (Conroy, 1996).

Indirect Indices of Abundance Based on Foraging and Commuting Bats

Indices Based on Visual Observations

Relative abundance of foraging bats may be estimated in some situations by deploying night vision devices and thermal infrared cameras (Fig. 7.12A). With one or more thermal infrared cameras directed upward, flight trajectories of individual bats can be determined by adjusting the playback speed of the recorded image showing trailing wing prints (Fig. 7.12B) or by applying computer vision algorithms to track individual bats (Fig. 7.12C). Owing to recent developments using two or more thermal or reflectance infrared cameras (videogrammetry) and computer vision algorithms, it is now possible to observe and quantify the number of bats in an established volume of three-dimensional air space (Holderied et al., 2005; Holderied and Jones, this volume). When stereoscopic optical tracking methods employ two or more cameras with acoustical tracking methods, the resultant three-dimensional imaging makes it possible to further quantify how many bats use a particular volume of air space.

Aided with spotlights, night vision devices, and flash photography (Altenbach and Dalton, this volume), distinct wing shapes and flight patterns may be used to visually

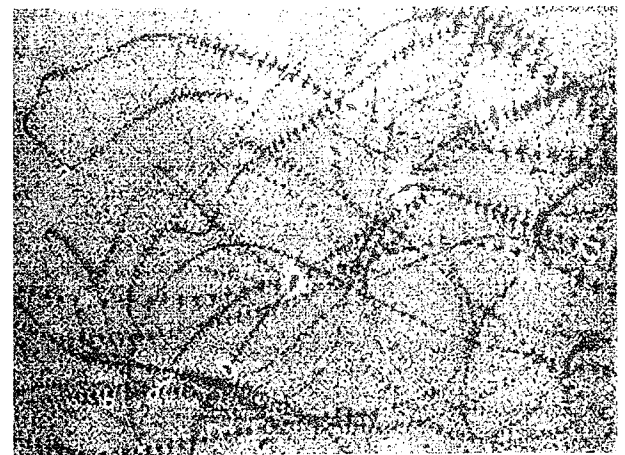


Figure 7.12. Infrared thermal imaging can be used to detect foraging bats. A, Brazilian free-tailed bats, *Tadarida brasiliensis*, are depicted as contrasting images against a uniform sky (image size of individual bats depends on distance from the camera); B, flight trajectories are shown as a series of "wing prints" in the camera's field of view; C, computer vision enhancement of foraging bats depicted with an automatic tracking algorithm. Photo A from Kunz et al., 2007; photo B from Kunz, 2004; photo C from Betke et al., 2008.

identify some species with limited degrees of confidence (Ahlén, 1980–1981; Limpens, 2003). With the exception of a few diurnal species (Speakman, 1995; Thomson et al., 1998), it is difficult to identify different bat species by sight alone while they are in flight. Species that have been provisionally identified by sight should be confirmed by capture and recordings of echolocation calls.

Indices Based on Acoustic Recordings

In regions where echolocating bats commute and forage (and especially where trapping is impractical or impossible), ultrasonic bat detectors have often proven useful for identifying bats to species (or genera) and for estimating their relative activity (Hayes, 1999; Kunz et al., 2007; Hayes et al., this volume). Bat detectors and associated software have considerably advanced knowledge on the foraging activity of microchiropterans (Brigham et al., 2004; Parsons and Szewczak, this volume). For example, acoustic surveys can provide valuable information on the nightly dispersal of bats along linear landscapes (Walsh et al., 2003; Limpens and McCracken, 2004), but users must understand the limitations, assumptions, and caveats of the study design, instrumentation, and analytical methods needed to achieve stated goals (Hayes, 2000; Gannon et al., 2003; Gannon and Sherwin, 2004; Hayes et al., this volume).

Quantitative methods now make it possible to distinguish most echolocating bat species by analyzing frequency ranges, changes in frequency with time, and pulse repetition rates (Parsons and Szewczak, this volume). In some situations, qualitative methods of assessing echolocation calls may be useful for identifying different species (O'Farrell and Gannon, 1999; O'Farrell et al., 1999a), but this approach largely depends upon reliable acoustic memory and lots of patience of the investigator. To avoid ambiguous species identifications based on qualitative assessments of echolocation calls [see Barclay (1999), and reply by O'Farrell et al. (1999b)], researchers are encouraged to use quantitative approaches (Brigham et al., 2004; Parsons and Szewczak, this volume). In addition to species-specific characteristics of echolocation calls, there may also be considerable variation in call characteristics with respect to sex, age, group membership, and individual quality (Obrist, 1995; Kazial et al., 2001; Kazial and Masters, 2004; Siemers et al., 2005), and further research is needed to explore the possibility of characterizing these parameters in other species.

Echolocation call-sequences can be characterized either as "bat passes" (the train and pulse produced by a bat passing through the air space sampled by the microphone(s)), and attacks known as "feeding buzzes." Recordings of bat passes generally provide information such as use of a particular habitat by microchiropterans, whereas feeding buzzes signify attempts by these bats to capture prey. However, to date, there has been no success in convert-

ing activity data based on echolocation calls to estimate the number of bats present, or for that matter yield information on relative abundance (M. B. Fenton, pers. comm.).

Indirect Estimates of Bat Abundance Based on Radar Reflectivity

The existence of 155 NEXRAD (NEXt generation RADar) or WSR-88D (Doppler) weather surveillance radars operated by the National Weather Service (NWS) for the National Oceanographic and Atmospheric Administration (NOAA) in the United States, including the territories of Guam and the Commonwealth of Puerto Rico, makes it possible to detect the intensity of reflected energy from objects in the atmosphere as well as the Doppler shifts of returned frequencies from moving targets. Similar weather surveillance radars have been installed for military and commercial television stations throughout the world, and archived data may be accessible to qualified researchers. In precipitation mode, these radar installations can detect birds, bats, and some concentrations of insects. When there is no precipitation detected, these radar operate in "clear-air mode" and sample the same volume of space more slowly, making it possible to detect reflected energy from very small reflectors such as insects and even dust and smoke particles (National Research Council, 2002).

NEXRAD Doppler radar can be used to quantify the timing, direction, velocity, altitude, and density of Brazilian free-tailed bats (Fig. 7.13; Horn and Kunz, 2008). It also has been used to identify the location of previously unknown roosts (e.g., bridge colonies). Horn and Kunz (2008) were able to locate previously unknown roosts of Brazilian free-tailed bats using NEXRAD Doppler radar when the bats emerged nightly from these sites. These data also have been used to assess both seasonal and long-term trends in relative population size of Brazilian free-tailed bats (Horn and Kunz, 2008). Notwithstanding, detection of biological targets aloft using NEXRAD Doppler radar is limited to bat species (and birds) that fly within the detection range above the horizon.

A new weather surveillance radar system currently under development by CASA (Center for Collaborative Adaptive Sensing; <http://casa.ece.uprm.edu/>) promises to be a valuable tool for assessing activity and relative abundance of foraging and migrating bats. Known as Distributed Collaborative Adaptive Sensing (DCAS) radar network, this system is being designed to monitor severe weather activity at relatively small spatial scales, and thus has the potential to aid in detecting biological objects aloft (bats, birds, and insects) at altitudes below the detection range of existing NEXRAD radar.

Recent developments of vertical profiler radar (A. Kelly, pers. comm.) have the capacity to detect individual targets up to 2.5 km above the Earth's surface, and thus has the

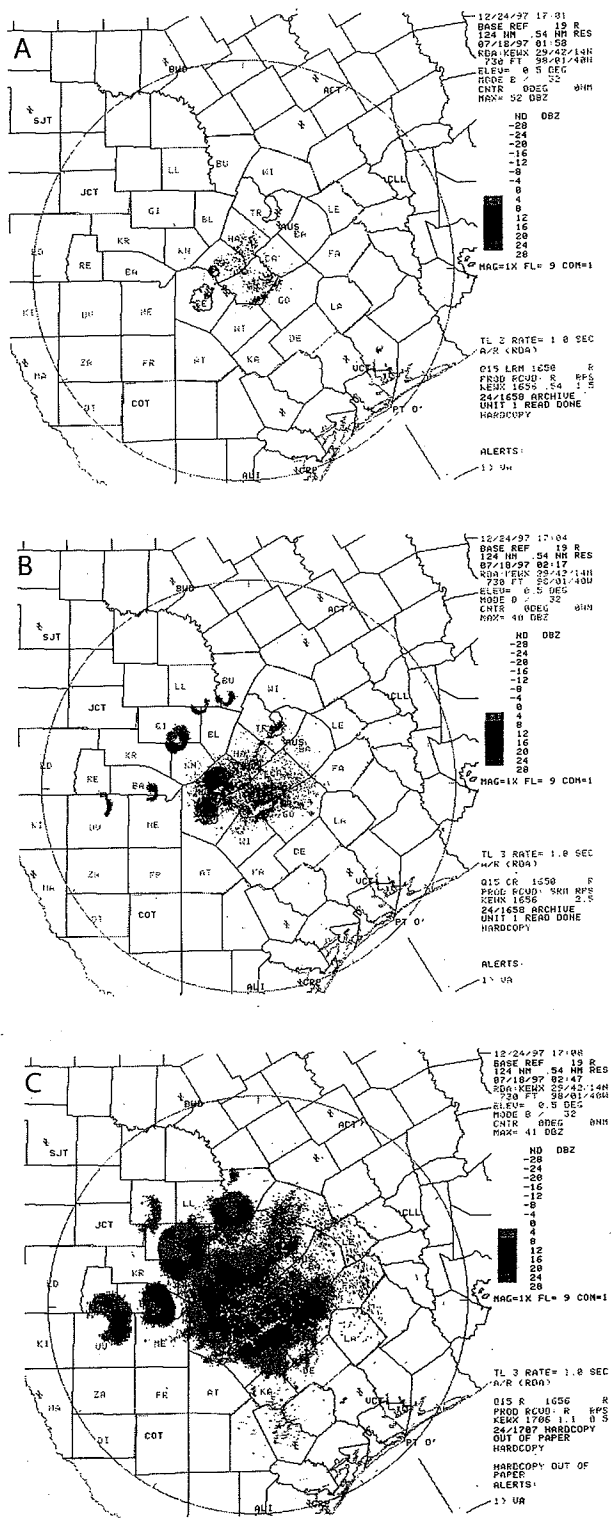


Figure 7.13. NEXRAD Doppler radar images of Brazilian free-tailed bats (*Tadarida brasiliensis*) dispersing from maternity roosts in south-central Texas. A, image of radar reflectivity shortly after the onset of nightly emergence. B–C, changing patterns of dispersal after emergence: B, 15 minutes after emergence; C, 30 minutes after emergence. After Kunz, 2004.

potential to assess relative abundance of bats, insects, and birds at specific altitudes and locations while they are dispersing, foraging, and migrating.

CONCLUSIONS

Censusing and estimating numbers of bats that occupy specific bat colonies or those that comprise local, regional, and entire species populations is a critical goal for assessing the long-term conservation and survival of bats (Kunz, 1982; Kunz and Lumsden, 2003; O’Shea and Bogan, 2003). Because most bat species are highly sensitive to human activities, especially in their roosts, it is essential for researchers to be sensitive to and take precautions to avoid activities that might affect colony behavior and, ultimately, the reliability of estimating colony and population size. In doing so it important for researchers to remain alert to possible affects of their research activities and ultimately to determine whether their research activities can be justified for the sake of gaining additional information at the risk of causing detrimental affects to colonies or populations being studied (Rudran and Kunz, 1996; Kunz, 2003; Hayes et al., this volume).

Hibernating bats are especially sensitive to human disturbance (e.g., Tuttle, 1979; 2003). Immediate adverse effects of research activities on hibernating bats may not be obvious to a one-time visitor, but both high metabolic activity and loss of body mass have been documented as resulting from frequent visits to hibernacula by researchers (Speakman et al., 1991; Thomas, 1995; Johnson et al., 1998). Thus, we suggest that repeated and prolonged visits to hibernating colonies be avoided (Tuttle, 1979; Keen and Hitchcock, 1980). Censusing hibernating bats is best achieved by counting each individual bat or group of bats as they are encountered, or by estimating the mean density of bats in several representative clusters, and then extrapolating this density to the total area of the cave wall or ceiling that is covered by bats. Censuses of hibernating bats should be limited to one census period every two years.

Similarly, maternity colonies of bats are highly sensitive to disturbance, and efforts should be made to avoid excessive activities during this period that might lead to abandonment or mortality. Young bats may be especially vulnerable at this time, especially when both adults and newborn young are disturbed; immature bats may be easily dislodged from the roost substrate when their mothers take flight in their efforts to escape. However, disturbance to bats by researchers at this time appears to vary with species, thus monitoring the affects of such visits to these sites should be a high priority. When neonates are present, it is less disturbing to the colony if visits by researchers are made after adults have emerged from their roosts to feed. Young bats can often be captured, handled, marked, and observed during the time females are absent

with minimal disturbance or induced mortality to flightless pups (see Kunz, Adams, and Hood, this volume). Once young bats have reached the weaning stage, and are capable of sustained flight, captures and observations within the roost appear to be less disturbing (T. H. Kunz, pers. obs.)

Traditional methods used to census bat colonies include visual counts within roosts and counts made during evening emergence and dispersal flights. While these methods are the current standards for censusing bats, improved capture and marking methods, and use of visual methods, have increased our ability to more accurately and reliably census and estimate the numbers of bats present. For many bat species, evening emergence counts provide the most reliable method for estimating colony size. Emergence counts are most effective at small colonies and where the emergence routes are known and can be monitored with an appropriate number of personnel. Successful emergence counts may be limited by inadequate lighting and poor visibility.

Where a given species forms relatively small colonies and roosts in open areas on walls and ceilings of caves, mines, and buildings, direct counts may be an acceptable method as long as prolonged disturbance can be avoided or minimized. Disturbance to roosting bats can be minimized by using low light-level video cameras, night vision devices, or reflectance and thermal infrared cameras and by reducing the number of visits to roost areas. Recently developed advanced detection and censusing methods, when used in combination with traditional census methods (roost counts and evening emergence counts), offer promise for estimating numbers of bats that form both small and large colonies. Molecular markers also hold considerable promise for estimating colony sizes and for estimating both demographic and effective population sizes of bats, especially rare and evasive species.

Mark-recapture methods have generally proven unsuccessful for censusing most bat species and populations because recapture rates are low and the assumptions of this method are rarely met. In addition, successful application of the capture-mark-recapture method may be compromised because some colonies of certain species frequently separate into smaller groups in fission-fusion societies, with some or all individuals shifting to alternate (and sometimes unknown) roost sites.

Methods used for estimating numbers of dispersing and foraging bats are more problematic and generally limited to making relative estimates of activity based on captures, observational, acoustic, or radar recordings. Devices suitable for assessing the relative abundance of dispersing and foraging bats include mist nets and harp traps. Photography and videography, using supplemental light sources, and thermal or reflectance infrared cameras can also be used for assessing the relative abundance of bats.

Reliable estimates of population size for gregarious species will depend on accurate and reliable estimates of colony size and an assessment of numbers of such colonies present in an area or region of interest. For other species, especially those rare and elusive taxa, the use of radiotelemetry, grids, transects, and intensive searches in discrete areas will be needed to adequately assess population sizes. Estimates of effective population size for all species will require intensive efforts to collect feces or tissues from individuals over wide geographic areas for establishing baseline population levels to compare with demographic estimates of population size. In the final analysis, accurate and reliable estimates of colony and population sizes and indices of abundance of bats are needed to assess both short-term and long-term impacts of anthropogenic changes on the earth's natural and managed ecosystems.

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