

Radiotelemetry

Techniques and Analysis

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RADIOTELEMETRY HAS BECOME AN IMPORTANT tool in studies of animal behavior, ecology, management, and conservation. From the first decades following the introduction of radio transmitters, radiotelemetry emerged as a prominent and critically important tool in wildlife science for the study of physiology, animal movements (migration, dispersal, and home range), survival, animal abundance, and resource selection. Advancements in technology since 1988 include subminiaturized transmitters, improved receiving systems, satellite receivers, and global positioning systems (GPS), as well as increased computer hardware and software capabilities to process data collected in radiotelemetry studies. These advancements have revolutionized radiotelemetry studies and made it possible to use this tool for increasingly smaller species.

The use of radiotelemetry requires an understanding of the techniques, limitations, and appropriate applications of this tool. Kenward (1987, 2001), White and Garrott (1990), Millspaugh and Marzluff (2001), and Fuller et al. (2005) provide reviews and detailed information on the technology, study design, and analysis of radiotelemetry for wildlife studies. This chapter provides an overview of considerations for using radiotelemetry in studies of the ecology and behavior of bats. We first discuss study design and the collection of radiotelemetry data, because these affect subsequent analysis, interpretation, and inferences. We then summarize and discuss analysis options. We focus primarily on techniques for working with moving bats because less attention has been given to this topic than to the use of radiotelemetry to locate roosts. Due to rapid developments in both equipment and analytical procedures, bat researchers should continue to review literature and electronic sources and to consult with colleagues and equipment suppliers to remain current.

DESIGN OF RADIOTELEMETRY STUDIES

Historically, bat telemetry studies were mainly descriptive. Although descriptive studies have a role for rare, elusive, or previously unstudied species, research studies designed to quantitatively investigate relationships between bats and their environment are now achievable.

The first consideration when designing a quantitative study is to identify specific objectives and the scope of inferences; these decisions will guide many of the remaining considerations, including whether radiotelemetry is an appropriate tool for achieving the objectives. The population of interest, geographic area, and scale of the proposed question will guide other decisions, including appropriate experimental units, measures of precision for hypothesis testing or model building, and numbers of individuals to be radio tagged (Garton et al., 2001).

Carefully designed studies maximize the amount and reliability of information obtained. Key considerations in radiotelemetry studies include selection of animals (i.e., randomly) for radio tagging, the number of animals, and the number of locations per animal (Worton, 1995; Seaman et al., 1999). Gender, age, reproductive condition, geographic location, and other unique characteristics contribute to variability or bias; therefore, stratification by sex or age is recommended when inference objectives dictate. Most analysis methods currently available for habitat studies assume random selection of individuals. If randomization and stratification are impractical, the research question, study design, or type of analysis may require modification to overcome violations of assumptions that may invalidate results. Analysis of movements may include differential patterns based on the individual, sex, age, season, and representative activity. Some bat species spend considerable time foraging in a relatively small area (Henry et al., 2002); others move rapidly from roost sites to more distant foraging areas (Kerth et al., 2001; Bontadina et al., 2002). Careful consideration of these factors will aid in determining appropriate time intervals to document movement rates and will guide the cost—and ultimately the feasibility—of a specific study. General guidance is available regarding numbers of animals (Alldredge and Ratti, 1986, 1992; Leban et al., 2001; Winterstein et al., 2001) and the number of locations per animal (Seaman et al., 1999; Kernohan et al., 2001). Having a proposed study design reviewed by a biometrician before embarking on any field work potentially avoids costly mistakes, such as biased data or inappropriate inferences, caused by deficient design. Ratti and Garton (1994) provide detailed information on experimental design; Kenward (1987, 2001), White and Garrott (1990), Garton et al. (2001), Kernohan et al. (2001), and Millspaugh and Marzluff (2001) provide additional information on radiotelemetry design issues.

Costs associated with radiotelemetry vary considerably depending on the objectives of the study and data analysis methods selected. Simple projects to find specific roosts may be relatively inexpensive, short term, and conducted by a few individuals; projects to quantify home range or foraging behavior require a much larger investment of personnel, equipment, and time to obtain adequate data to make inferences. To determine the feasibility of a study, a budget based on study objectives, including sample size and number of relocations required, should be developed early in the design process. Project cost estimates should include the purchase of equipment (transmitters, antennas, and receivers), salaries and expenses for field personnel, and transportation (e.g., vehicles, aircraft). If the budget is limited, some objectives will not be feasible and either additional funding should be sought or study objectives should be reevaluated.

EQUIPMENT AND TECHNIQUES FOR RADIOTELEMETRY PROJECTS

Equipment for Telemetry Systems

The basic components of a radio-tracking system include (1) a transmitting system consisting of a radio transmitter, a power source, and a propagating antenna, and (2) a receiving system including an antenna, a signal receiver, and a power source. Although several types of radiotelemetry systems are currently used in wildlife research, including very high frequency (VHF), ultra high frequency (UHF), satellite, and GPS, VHF radiotelemetry is the only type currently available that meets the size and weight restrictions for smaller bat species. Technology, including use of satellite tracking and GPS telemetry, is rapidly advancing; the minimum weight of currently available equipment is approximately 9.5 g for solar-powered platform transmitter terminal (PTT) units and 20 g for battery-powered units. GPS-enabled PTTs weigh a minimum of 30 g. These weights may allow use of these methods for large species but render them unsuitable for smaller species. Current satellite technology is considered less accurate than VHF; differentially corrected GPS telemetry theoretically increases accuracy to ± 5 m. However, GPS units are also several times more expensive than standard VHF and non-GPS satellite units. These technologies hold promise for future applications, as units will likely decrease in size and expense.

Transmitters

Transmitters attached to microchiropterans typically weigh less than 1.1 g (Barclay et al., 1996; Brigham et al., 1997; Lacki and Schwierjohann, 2001; Willis and Brigham, 2002) and have proportionally small batteries and weak signals that place strict requirements on the receiving equipment, especially on the receiving antenna. Transmitters weighing 0.25–0.65 g, with magnetic reed switch

or manual activation, are available from several sources (Appendix 3.1). Larger transmitters, suited to larger species, provide significantly longer battery life and thus longer tracking time (for bats over 75 g, a 2–3 g transmitter lasts 10 weeks or longer; Fuller et al., 2005).

Transmitters that provide temperature measurement of the bat use a sensitive thermistor that varies the pulse rate of the transmitter. The pulse rate is determined with the aid of a stopwatch and converted to a temperature using a calibration curve. The system is sensitive to 0.1°C and does not increase the volume of the transmitter.

Telemetry studies of small bats typically use surgical glue or a similar nonirritating adhesive to attach the transmitter between the scapulars (Wilkinson and Bradbury, 1988). Some species are particularly adept at grooming the transmitter off before the transmitter fails. Many bat species chew at the contact between the transmitter body and the antenna, which can fray or become detached from the antenna. Strengthening this junction with glue, epoxy, or heat shrink-wrap is sometimes enough to maintain the integrity of the device. Other species can destroy multifilament antenna wire, requiring the use of single strand antennas. The tracking period for bats wearing small transmitters can be affected by the attachment adhesive, the amount of chewing on the transmitter, or molt condition, as well as battery life.

For some larger species of bats, transmitters can be attached to collars or necklaces (Spencer and Fleming, 1991). These devices should be shaped carefully to fit the animal's neck contours and must be sufficiently wide and smooth to evenly distribute the transmitter mass to avoid cutting or chafing. The fit must accommodate swallowing and seasonal changes in neck circumference. The material must be durable yet sufficiently flexible to respond to neck, shoulder, or chest movement. The mass of the transmitter and material should be positioned to keep it from interfering with the animal's natural movements (Fuller et al., 2005).

Animal handling and transmitter attachment will have some effect on all species, and the effect can be expected to differ among age groups and physiological status of the individuals (Kenward, 2001). Effects on flight may be either physiological or related to transmitter mass and drag (Pennycuick et al., 1989; Hickey, 1992). Aldridge and Brigham (1988) found an inverse relationship between a bat's increased mass due to the attached radio transmitter and its ability to maneuver. They suggested that decreased maneuverability is likely to result in bats choosing open sites over cluttered sites for foraging. Neubaum et al. (2005) found that adult female big brown bats can carry transmitters that are 5% or less of their body mass without long-term impacts on survival, reproduction, or body mass, which is consistent with literature from other taxa (Withey et al., 2001). The current recommendation by the American Society of Mammalogists (1998) is that total

mass of the transmitter, adhesive, and any other markings should weigh less than 5% of the preattachment weight of the bat. In the case of pregnant females, special consideration should be given to whether attachment is appropriate at all. If the female is tagged, preattachment mass should be estimated from the normal mass range for the species, or by subtracting the estimated fetal mass based on fetal development (a full-term fetus may represent 20–30% of female body mass; Hayssen and Kunz, 1996). It is, therefore, important to justify the need, understand the impacts, and minimize complications of transmitters for scientific, economic, humanitarian, and legal reasons (Murray and Fuller, 2000; Withey et al., 2001). A "common sense" rule is used by many researchers: (1) always consider the ethics of attaching tags; (2) consider the behavior, load carrying capacity, and wing metrics of the study animal (load carrying ability varies considerably); (3) aim for a tag that weighs less than 5% of the bat's body mass; and (4) tags should definitely be less than 10% of body mass if carried for more than a few days (O'Donnell, 2006).

Receivers

Receivers must be able to detect and distinguish signals of specific frequencies. The receiver must amplify the weak signal from a bat transmitter and reject similar frequencies from stronger sources. A basic receiving system consists of a battery-powered receiver, a receiving antenna, cables to connect the receiver to the antenna, and accessories that may include headphones, brackets for mounting receiving antennas to vehicles and aircraft, scanners to enhance searching for numerous signals, specialized recorders to aid in data collection, and various types of software.

Radio receivers designed for wildlife applications are available from a number of companies (Appendix 3.1). Because of the weak signal produced by bat transmitters, receivers with the highest sensitivity are desirable. Typical receivers cover bandwidths of 1 to 45 MHz (Fuller et al., 2005). Standard receiver components include a power switch; controls for gain, channel, band, and fine frequency adjustments; and jacks for an external antenna, headphones, a recorder, and external power. Some receivers also have a volume control. Volume differs from gain in that an increase in gain increases signal sensitivity (up to a point beyond which the sensitivity does not increase), whereas increasing volume affords no greater signal sensitivity. Separate gain and volume controls allow the tracker to set the gain high and reduce the volume so that the background hiss is reduced without sacrificing sensitivity. A fine frequency adjustment is useful because signal drift can occur in the field due to temperature and battery fluctuations (Mech, 1983). Handheld receivers (352 g) that can store up to 999 frequencies are also available. Receivers that can store about 100 channels are suf-

ficient if a maximum of about 20 bats are tagged in a session (this number will cover initial tagging, retagging during the session, and beacons). Some receivers have channel memories and are programmable; they can automatically scan for several frequencies at user-defined intervals from 2 seconds to 10 minutes (Fuller et al., 2005). Some receivers require frequencies to be entered by dials whereas others are digitally programmable. Receivers may also include gauges indicating battery power and signal strength. Most portable receivers are powered by rechargeable batteries or can be powered externally from vehicle power outlets.

Antennas

The antenna serves to both increase the gain (signal gathering capacity) of a receiving system and to assist the operator in determining the direction from which a signal is coming. A receiving antenna has a three-dimensional pattern of power oriented in relation to the element(s) of the antenna (Fuller et al., 2005). Larger antennas (more elements) generally yield greater gain and directionality but at the expense of portability. Selection of the appropriate antenna is important; even in ideal situations only half of the signal's power captured by the antenna is actually delivered to the receiver (the other half is re-radiated) (Samuel and Fuller, 1996). The signal's energy is transferred from the antenna to the receiver by a coaxial cable that shields the electronic signal against extraneous noise and helps minimize signal power loss (Samuel and Fuller, 1996). If signal loss along the cable leading from the antenna to the receiver (transmission line) is too great, preamplifiers can be incorporated between the antenna and the transmission line (Kenward, 1987).

The simplest kind of receiving antenna is a straight wire or "dipole" attached to the receiver's antenna jack. Dipole antennas are omnidirectional and have limited range, and are therefore most appropriate for presence/absence studies over short distances (Mech, 1983).

A multielement Yagi antenna consists of a horizontal length of metal (the beam) with 3 to 17 perpendicular lengths (the elements) attached to it, all in one plane. The length of the elements and their spacing depend on signal frequency. Yagi antennas are directional, with shorter elements at the forward end of the antenna. Maximum sensitivity is in the "front" direction, but there is also a somewhat reduced peak 180 degrees away, in the "back" direction. The ratio of these two sensitivities, called the front-to-back ratio, will determine how easily the signal direction can be discerned. As this ratio increases, the probability that 180-degree errors will occur is reduced. As number of elements is increased, front-to-back ratio increases (Fuller et al., 2005).

Another type of receiving antenna is the H-antenna. This antenna is often used for handheld applications because it is smaller than the Yagi; however, it has reduced

gain and has a poor front-to-back ratio. Although it has been successfully used with many taxa, the H-antenna does not work well for triangulation of bat locations.

Factors Affecting Transmitter Signal Detection and Accuracy and Precision of Acquired Azimuths

Accuracy is the degree to which the estimated location is different from the actual location. Precision is the repeatability of measurements. Precise but inaccurate azimuth measurements are just as bad as imprecise but sometimes very accurate measurements. Inaccurate telemetry data are misleading and are as counterproductive as few, or no, data. Not understanding factors that affect signal detection, accuracy, and precision of azimuths can cost time and effort in homing studies and can result in poor data in triangulation studies. There are usually no, or few, opportunities to confirm a bat's actual location using triangulation (see section Increasing Signal Detection and Reducing Error for ways to maximize accuracy). Results and inferences from studies poorly planned or executed can be wrong, but if published, become accepted by the scientific community.

Telemetry Systems

Recent advances in the design of antennas and receivers have led to a refinement of VHF telemetry tracking and to a better understanding of potential problems. Reliable equipment is a must, and understanding the characteristics of radio wave propagation is essential to success. Design of the antennas for both transmitter and receiver systems is important because it determines how well energy is transferred from one antenna to the other. Factors affecting this transfer include gain, directionality, and polarization.

Actual radiated signal strength will diminish as the transmitting battery's power drops or damage occurs to the transmitting antenna. A damaged receiving antenna (bent elements), cable, or receiver will diminish effective sensitivity of the receiving equipment. Frequency drift in the transmitter occurs often; the result is the perception of diminished signal strength or failure to detect the signal at all until the receiver is adjusted.

The precision of acquired azimuths for a receiving antenna system is specific to the particular design. Larger antennas have several advantages over smaller ones. As the number of elements increase, sensitivity (gain) increases, and directionality improves. As a result, transmitter signals can be detected at greater distances, and the inherent error in precision due to the antenna decreases.

Polarization refers to the orientation of the energy field (radio wave) produced. As a bat flies, the relative positions of the transmitting and receiving antennas change, causing variability in the efficiency of energy transfer from the transmitter to the receiver. This causes the apparent signal strength at the receiver to vary. Signal strength ap-

appears stronger when the elements of the receiving antenna are parallel to the transmitting antenna and weaker when they are perpendicular. The bat's flight pattern will cause the relative polarization to change constantly and rapidly. Because it is not possible to predict at any given instant what the polarization of the transmitting antenna will be, it is not possible to compensate for polarization with the receiving antenna. This problem can be mitigated by selecting the highest signal strength with a minimum gain setting to ensure that the perceived nulls are the true nulls and not a change in polarization.

For triangulation, determining the azimuth as accurately as possible is crucial. A compass attached in line at the mast and in line with the antenna saves valuable time and increases accuracy and precision of azimuths. An electronic compass calibrated to eliminate interference from mounting materials and attached to a digital readout is preferable (Amelon et al., 2003), but a magnetic compass also works. Electronic compasses that consistently provide readings with an accuracy of ± 0.5 degrees are commercially available (Appendix 3.1).

Environmental Factors

Propagation characteristics of radio waves are subject to many variables that affect the range and performance of a system. The two main considerations are (1) partial or complete loss of the signal along the transmission path between the transmitter and receiver and (2) signal path alterations. Factors affecting signal loss are obstacles (trees, buildings, terrain) and power loss (humidity, temperature). The signal path can be altered by terrain, trees, or buildings, causing radio shadow, reflection, or refraction. Fresnel effect and multipath can severely limit the range of reception. Magnetic anomalies in rocks near the receiving station can disrupt magnetic compass readings. Many phenomena affecting radio signals are beyond the scope of this chapter; additional information can be obtained from sources in Appendix 3.1.

Ideally, telemetry readings are "line of sight" (LOS), where the radio wave travels directly from the transmitting antenna to the receiving antenna without obstructions. Maximum line-of-sight transmission distance is determined by antenna sensitivity and height. In LOS transmission path, signal power decreases in proportion to the square of the distance (Matthews, 1965). In actual practice, power drops off much faster because of attenuation due to factors including the ambient humidity, the animal's body, the Fresnel effect, and local soil, water, and geology.

Radio shadow (signal is blocked), refraction (signal bends), and reflection (signal bounces) are well-known problems that affect signal detection and cause errors in azimuths. The tracker is usually unaware these factors are influencing the signal's path and is unable to compensate during the azimuth's acquisition, even if a problem is suspected. Preventing or minimizing the influence of

these factors is discussed in the section Increasing Signal Detection and Reducing Error.

On flat terrain, one might assume good signal detection and LOS, and therefore accurate azimuths; however, this is not always the case. Multipath can cause severe interference, which can be mitigated by elevating the antenna.

Acquiring and Estimating Locations: Techniques

Telemetry has two main techniques: homing and triangulation. The most appropriate technique depends on the objectives of the study. The equipment and number of people needed, and therefore the cost and complexity, differ between the two techniques.

Homing

Homing involves searching for a stationary transmitter and "homing" in to obtain the location by direct observation. The study objective can be to locate a day roost, night roost, or a feeding station. Visual observations of radio-located animals provide the best confirmation of the accuracy of the location data, although they are often difficult to obtain with many species of bats. Homing uses directionality and signal strength to move toward the signal. When a signal is detected with a minimum gain setting, the animal should be relatively close. Using the receiver with minimum gain or without the antenna, the tracker can usually isolate the roost location. With practice, foliage roosting species may be visually located with binoculars; the antenna of crevice-dwelling species may be seen protruding from under bark or from a tree or rock cavity, or may be heard. For species that roost in colonies, watching the roost at dusk or with night vision equipment may allow for visual roost confirmation. Mine/cave obligates are more difficult to locate in this manner because the signal is usually dampened by the earth.

A variation of the homing technique is to circle the signal to within a small area and assume the animal is within the area (White and Garrott, 1990). This "close approach" method has been used by Law and Lean (1999) with the common blossom bat (*Syconycteris australis*), by Smith and Racey (2005) with Natterer's bats (*Myotis nattereri*), and by O'Donnell (2001) with New Zealand long-tailed bats (*Chalinolobus tuberculatus*).

Aerial tracking is a special instance of homing in which aircraft are used to cover large areas systematically. Aircraft tracking has recently been used to follow bats as they leave their hibernacula in New York (Hicks et al., 2002). Kenward (1987, 2001), Fuller et al. (2005), and Mech (1983) have provided detailed information on these techniques.

Regardless of estimation methods, careful field calibration tests to determine accuracy of locations are required to use these estimates unless a visual verification can be acquired.

Triangulation

Triangulation is used to obtain locations of moving or stationary bats. Study objectives can be to identify home ranges, foraging areas, or commuting routes; this technique is also the most efficient way to identify locations of day-roosts and night-roosts for far-ranging bats (locations are subsequently confirmed by homing). In this method, bearings on the transmitter signal are determined from two or more geo-referenced locations (preferably at angles approximating 90 degrees). The polygon created by the intersection of the azimuths and their associated error (the error polygon) theoretically contains the animal's true location. Obtaining good data through triangulation is considerably more difficult than through homing. For this reason, a more detailed discussion about data collection by this method is presented later in this chapter.

Locating Receiving Stations

Where ample road access permits, mobile vehicle systems are especially useful to obtain the best position for triangulation or to cover long distances (Fig. 3.1). Antennas for mobile tracking are limited to a size suitable for the vehicle used.

Remote study areas can require trackers to hike to locations not otherwise accessible. Specialized equipment designed to be lightweight, collapsible, and easily field-assembled is necessary. A tripod can be modified to accept the bottom of a 2-m aluminium mast, which holds a five-element Yagi antenna and the antenna for a two-way communication radio. The mast frees the tracker from holding the antenna in hand the entire night, minimizing observer fatigue. Mobile trackers can hike, stopping as frequently as necessary to obtain an azimuth while holding a three-element Yagi.

Aerial systems in which Yagi or H-antennas are mounted on each wing strut are useful for areas difficult

to access by foot or vehicle or when a bat moves long distances very quickly. Complete descriptions of the process of aerial tracking can be found in Whitehouse and Steven (1977) and Mech (1983).

Null-to-null Method of Obtaining Azimuths

Azimuths on bats in flight should be obtained using the null-to-null method. Even in a high-gain antenna, the peak (signal sounds strongest) is perceived over several degrees. In the null-to-null method, azimuths are obtained by first rotating the antenna to the approximate direction of the strongest signal. Nulls are points to either side of this estimated peak azimuth where the signal strength is undetectable. The antenna must be moved back and forth several times to find the "real" null, as polarization may be changing as the bat is flying. The azimuth to the signal is determined by bisecting the angle between the nulls. Turning the gain down so that the nulls fall within about a 30° angle of the suspected azimuth makes bisecting the angle easier.

Error Polygons

An error polygon is created when an estimated location is determined through triangulation. The polygon can be calculated, resulting in a measure of precision for the point estimate equivalent to the area of the polygon. The size and shape of the error polygon is determined by (a) the precision of the directional antenna, (b) the distance between the receiving points, (c) the distance of the transmitter from the receiving points, and (d) the angle of the transmitter from the receiving points. The most accurate estimate of an animal's location is usually obtained by multiple receiving stations that are close to the animal and at approximately 90 degrees from each other. For habitat studies, the error polygon must be small enough to accurately place the animal within a single habitat patch. If the estimated location is near a patch edge, the number of tracking stations should be increased and stations moved in closer to decrease error size. Radiotelemetry studies should include and describe procedures used to estimate errors as well as an indication of the magnitude of the errors. White and Garrott (1990) provide comprehensive information on methods for error calculations in radiotelemetry studies. Withey et al. (2001) describe methods for site-specific evaluations. Additional information on minimizing error polygons follows this section.

Many software programs that calculate error polygons require three or more azimuths. Two-way crosses, in which the azimuth error can be estimated, will also have an associated error polygon that can be estimated by plotting. White and Garrott (1990) and Fuller et al. (2005) provide comprehensive discussions of triangulation techniques; they also discuss newer methods that are replacing error polygons.



Figure 3.1. Photograph of two five-element Yagi antennas mounted on a vehicle in parallel design.

Increasing Signal Detection and Reducing Error

Accuracy of location estimates has potentially serious impacts for interpretation of resource selection. A bearing error of one degree (most bearings have greater error) translates into a linear error of 17.5 meters per km distance from the receiving unit (Fuller et al., 2005). When the entire data set is derived from triangulated bearings whose accuracy cannot be verified, minimizing error is critical. Because transmitters frequently are groomed off the animal after several days, acquiring many locations within that time frame is also critical to ensure sufficient data points.

Estimation of animal locations is affected by variability in radio wave propagation, equipment performance, environmental factors, and operator factors, as well as the movements and behavior of the animal (Fuller et al., 2005). The techniques for minimizing error and increasing sample size discussed below will contribute greatly to the success of the study.

Elevation of Antennas

Receiving stations should be situated on the highest points in the study area to detect the greatest number of signals. In hilly or mountainous terrain, radio shadow, reflection, and refraction can be serious problems; elevating stations is the only way to reduce these problems. In flat areas, multipath interference can often prevent detection of a direct-path signal; signal detections will increase by elevating stations.

An elevated tower system can greatly enhance reception distance of small bat transmitters (Amelon et al., 2003). Stationary tower systems can be fixed or rotating to record presence and absence data or rotated to determine the direction of the signal (Smith and Trevor-Deutsch, 1980; Mech, 1983). White and Garrott (1990) and Woeck et al. (2002) described techniques for determining favorable locations for stationary receiving stations to increase ac-

curacy and coverage. Samuel and Fuller (1996) discuss the positioning of antennas with respect to vegetation, large buildings, obstructive terrain, and its effect on the range of signal reception.

Multiple Receiving Stations

Multiple tracking stations can decrease error polygons (i.e., increase precision) of triangulations and increase confidence in the accuracy of estimated locations. If estimated locations require three-way crosses, more than three tracking stations are usually needed; three azimuths do not always cross, and the bat is not always detected by all stations. In our experience with hike-in trackers, six tracking stations are usually the minimum needed. If the target species remains in a relatively small area, most azimuths will be LOS. Tracking stations can make adjustments in location and three or four stations may be sufficient. Ideally, there should be enough observers so that the perimeters of each bat's range can be established. Researchers without funds for sufficient trackers risk a poor data set; changing objectives or obtaining additional funds is recommended.

Under LOS conditions, azimuths should converge on the "real" position. If a location is estimated from two azimuths, the validity of the position cannot be confirmed. One or both azimuths could be LOS, or they could be reflected or refracted. Even with three azimuths, the triangulated position can be unclear if the three azimuths do not all converge, a common situation. It is the agreement among several receiving stations on the point of convergence (the triangulated position) that strongly suggests the estimated position is reliable. The example in Figure 3.2 shows that the position estimated from six azimuths is about 2.5 km from the position estimated from two azimuths.

Simultaneous Azimuths

Foraging bats move quickly, therefore, azimuths from multiple trackers must be obtained simultaneously for

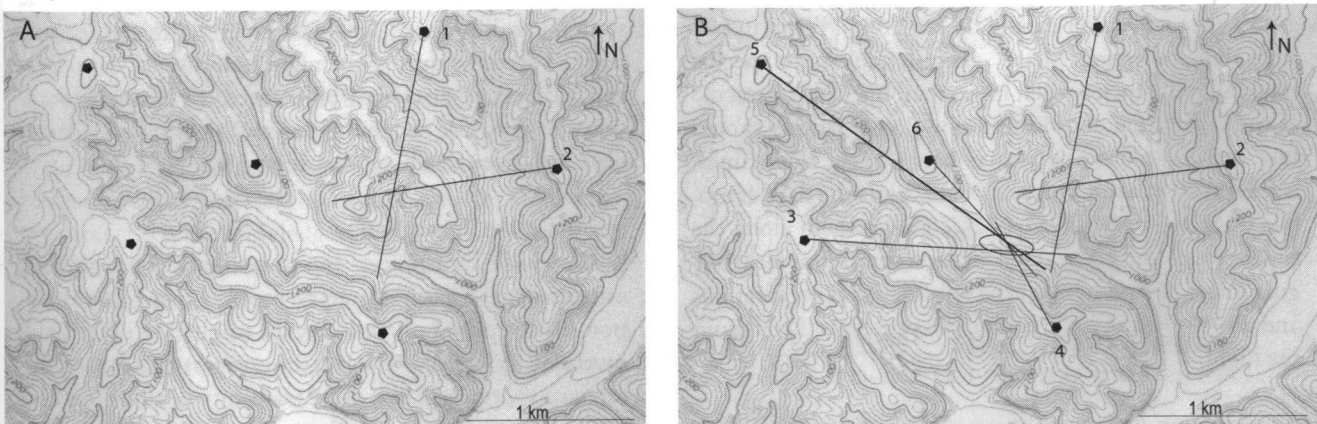


Figure 3.2. Estimated bat location using azimuths: A, estimate from two receiver locations; B, estimate using azimuths from six receiver locations.

triangulations to produce accurate locations. Good results require practice and coordination of observers. Trackers need synchronized watches and/or radio contact with other trackers and/or a coordinator (discussed below). A concise radio protocol or systematic sampling approach allows coordination with a minimum of distractions. For a specific signal frequency, an azimuth is determined by finding the range of the nulls. The tracker makes a final determination of the azimuth by bisecting the angle between the nulls at a specific time, and then a compass azimuth is taken and recorded over the next few seconds. The time between azimuths is used to relocate the nulls and repeat the process. Trackers note their degree of confidence for each azimuth (e.g., 128°, ~128°, SE). Azimuth, gain level, signal strength, and other data (e.g., signal lost abruptly) are recorded. An alternative technique for situations in which bats move to foraging locations in which a single "base" is not effective uses teams of three or more trackers assigned to bats foraging in close proximity. Each team operates with a systematic sample scheme for the bats foraging near their location. Readings are recorded for each bat on a predetermined schedule to obtain similar numbers of locations for each bat in track. Trackers communicate with each other when a bat goes out of range. During slower periods, one team member plots azimuths. This technique works well with vehicular and stationary tower systems and ensures locations on all bats in track are obtained throughout the night.

In order to coordinate and make preliminary decisions about the night's tracking locations and strategy, each team needs to have a map of the study area on a laptop computer, with tracking stations and beacons marked. Either a GIS interactive software program that plots bearing on georeferenced map or at least a minimal set of computer drawing tools is required to determine if azimuths are converging or if adjustments need to be made.

Coordinating Multiple Trackers

If budget and communication systems permit, a central dispatch, or "base," station that coordinates and guides data collection during the night will result in efficient data collection. "Base" assigns trackers to specific tracking frequencies when more than one bat is detected at the same time and decides how long trackers should take azimuths on a particular bat. During slow times, trackers call in azimuths, and "base" plots the data. If mobile trackers are deployed, "base" guides them along the easiest route and keeps them at angles optimum for triangulation. The base station can coordinate tracker locations and deal with safety and equipment problems throughout the night.

High-gain Antennas

Greater reception range and more precise directionality can be obtained by using larger antennas and elevating

receiving antennas (Anderka, 1987). As the number of signal detections are increased; azimuth error and error polygon size is reduced.

Typical systems used for fixed telemetry stations include 5- to 14-element Yagi antennas (Banks et al., 1975; Kenward, 1987, 2001). Five-element antennas have been used for over 15 years by two of the authors (DD, SW) with routine detection of 1.1-g transmitters at 16 km. For small transmitters (0.5–0.6 g) in forested situations, antennas with more elements improve both accuracy and precision of azimuths and allow transmitters to be detected routinely at 2–5 km, and for high-flying species, at up to 15 km. A phased array in a peak configuration (bats move too quickly to use a peak-null configuration) can also be deployed in one or more strategically located, elevated locations. Trackers on foot use three-element Yagis, which are superior to H-antennas for bat telemetry; both flexible-element and folding-element types are available.

Beacons

The accuracy of azimuths can be greatly affected by the terrain, magnetic anomalies, condition of the equipment, and the operator. Accuracy can be determined by the precision and bias of repeated azimuths taken in field tests (White and Garrott, 1990). These values are fundamental to determining location error (Amlaner and McDonald, 1980; Cederlund and Lemnell, 1980; Anderka, 1987; Kenward, 2001). Parameters of precision and bias, as well as detecting equipment problems, can be determined through the use of several reference beacons. These are transmitters (the size used in the project) attached to an AA battery and placed in elevated, geo-referenced locations. Prior to the start of the project, beacons can be used to delineate regions of LOS reception and regions where radio shadow, refraction, or reflection occurs. At the beginning of each night, trackers take azimuths on beacons and verify the system is properly calibrated. Equipment problems can be identified and corrected before the tracking begins, thus preventing loss of data. If necessary, the station can be moved, operator error addressed, or azimuths corrected during the night's plotting of data. Beacon locations that cannot be detected by particular stations may provide insight to bat locations obtained, or not obtained, from those stations during the night.

Fast-pulse Transmitters

Fast-pulse transmitters (up to two pulses per second) are beneficial to bat telemetry projects using triangulation. Faster pulses allow a tracker to quickly obtain azimuths on flying bats. The battery on a fast-pulse transmitter has a shorter life. Fast-pulse transmitters allow trackers to consistently take azimuths once a minute. Depending on study objectives, the benefits of using fast-pulse transmitters may justify the shortened battery life. Transmitter

manufacturers can adjust the pulse rate and battery life to best fit a specific study.

Strategies for Location and Type of Tracking Stations

The techniques and equipment used to acquire tracking locations may differ based on the study objectives and geographic scale of interest. Broader-scale movements, whether daily (species that fly directly to distant foraging locations or switch day-roosts) or seasonal (between winter and summer locations), may require greater emphasis on techniques (e. g., vehicle or aerial systems) with less initial emphasis on accuracy of location data. Long-range data is also possible with stations on elevated sites. For example, lesser long-nosed bats (*Leptonycteris curasoae*) have been tracked to foraging areas and day-roosts about 32 km from the capture site using this method (M. Bogan, USGS, pers. comm.).

Specific foraging patches, or specific plant locations in the case of nectar feeding species, require locations with fine enough resolution to describe the resources used by the bat. Moving fixed receiving stations closer, both to each other and to the bat, is one solution. Another solution is to have at least two trackers on foot using three-element Yagis and GPS units and in communication with either each other or a coordinator. Depending upon the objective, homing can be then used to obtain a visual confirmation of the bat's location.

Increasing Data Quantity

Due to the short life of most transmitters, continuous-interval or short-interval discontinuous sampling are the best options. Longer time intervals yield too few estimated locations for meaningful analysis. In order to obtain adequate usable locations—and to make valid inferences—bats should be tracked all night long for as many nights as possible, preferably until most or all transmitters are dropped. Fast-pulse transmitters (discussed earlier) may also increase the number of locations acquired; however, if the analysis method requires independent locations, closely spaced readings may be problematic.

Additional Factors Affecting the Success of a Telemetry Project

In addition to developing a good study design, other advance work is necessary to execute a successful telemetry project. Good knowledge of the study area, permission for access and pre-locating potential tracking stations (those with good radio coverage) and access to stations (road or cross-country hiking) are essential.

The tracking crew will make or break the project; they produce the entire data set. Hiring seasoned field workers who are conscientious, detail-oriented, and work well alone and with others, and then training them and paying them well, will result in quality data sets.

Trackers with sufficient training before the start of the tracking session will have fewer problems and collect more and higher-quality data during the session. Training should include radio theory and how it applies to tracking, practice with the equipment on stationary beacon transmitters, and a simulated tracking session on multiple beacons being moved in cars or on foot.

Bat radiotelemetry projects that include both roosting and foraging require a crew large enough to allow for day and night shifts. By having a day and night crew, efficiency of the project is improved; day staff will locate roosting locations and can be available to obtain equipment repairs and to determine if receiver locations or timing sequences from the previous night need adjustment. If duration of transmitters is short, work hours are long during the life of transmitter. Adequate staff is needed to ensure crews are able to get sufficient rest for safe operations and accurate data collection.

ANALYSIS AND APPLICATIONS OF RADIOTELEMETRY DATA

To assess typical applications of bat radiotelemetry studies, we conducted a literature review of studies published between 1983 and 2004 using *Wildlife and Ecology Studies Worldwide* (online database from NISC, the National Information Services Corporation; <http://www.nisc.com>). Sixty-three peer-reviewed studies were categorized as technology development or advancement, effects of transmitters, simple movement, behavior observation, habitat use and/or home range, or measuring a physiological process (Fig. 3.3). Most studies (90%) were one season in duration, followed a descriptive design, and monitored fewer than six bats of a particular demographic group. Habitat use and observation of roosting or foraging behavior objectives accounted for much of the increase between 1998 and 2004. The majority of habitat use studies

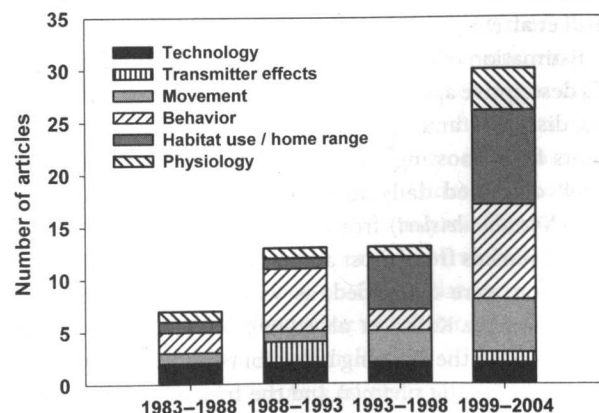


Figure 3.3. Type and number of radiotelemetry studies reported in the literature from 1983 to 2004. Counts of peer-reviewed publications were obtained from a search of NISC's *Wildlife and Ecology Studies Worldwide* database, which yielded 63 articles.

focused on roost site selection using methods other than triangulation. This focus in part was due to limitations associated with potential effects of transmitters on flight behavior when using transmitters exceeding 5% of body weight and partly due to lack of availability of transmitters within the 5% rule for many species. Recent introductions of micro-sized transmitters coincide with increasing numbers of bat habitat use and movement studies. The remainder of this section focuses on applications of radiotelemetry data to studies with objectives relating to movement, home range, or habitat use.

Analysis of Spatial and Temporal Resource Use

Radiotelemetry is an appropriate tool to obtain spatial and temporal data for bats over various geographic scales. Research objectives, geographic scale of interest, accuracy of location estimates, and frequency of relocations determine appropriate analytical approaches for spatial and temporal data (Fuller et al., 2005). Early spatial studies focused on general distances moved by bats between roosts. More recently, spatial and temporal information has been related to foraging (Henry et al., 2002; Lacki et al., 2007), seasonal movements (Kurta and Murray, 2002), and daily movements (Bontadina et al., 2002).

Movement

Many movement analyses require plotting locations by individual bat. Movement rates are calculated from sequential locations (distance moved divided by time interval). Several approaches to analysis of movements are fully described by White and Garrott (1990). Kernohan et al. (2001) categorized approaches to modeling animal movements as (a) descriptive approaches that estimate or describe movement patterns without reference to an underlying model, (b) general movement models, and (c) a priori mechanistic models that incorporate biological attributes of the species under investigation. Additional information on biological and mechanistic models can be found in McCulloch and Cain (1989), Turchin (1996), Focardi et al. (1996), and Moorcroft et al. (1999).

Estimation of daily movement distances is an example of a descriptive approach; no underlying model is assumed and distances and routes are used to determine movements from roosting areas to foraging areas. Shiel et al. (1999) described daily foraging movements of Leisler's bats (*Nyctalus leisleri*) from two nursery colonies in Ireland; distances from roost and duration of foraging bouts by season were quantified, as was dispersal distance of two juveniles. Kalko et al. (1999), working in Panama, characterized the foraging behavior of d'Orbigny's round-eared bat (*Tonatia silvicola*) and the fringe-lipped bat (*Trachops cirrhosus*) using descriptive movement approaches.

Movement locations over shorter time intervals are necessarily spatially autocorrelated to depict incremental changes. The sampling frequency relative to flight speed

and diversity of the flight pattern of the bat influences how well the actual path can be represented (Pace, 2001). Sampling frequency must be frequent enough to capture the important characteristics of the movement path and to account for location errors and other noise in the data. Variability also occurs from plotting, coordinate system, and operator errors. Because of these errors, movement paths are estimates of true movement paths. Turchin (1991, 1998) discussed sampling frequency with respect to error-free location data and foraging behaviors. Pace (2001, 2000) described a moving window approach to smooth errors in location estimates based on pooling locations over short time intervals.

Home Range

Movements of many animals, including bats, can be viewed as use of an overall area representing relocations in space and time. The concept of home range originated by Burt (1943) is "the normal area used by an animal in its life activities." This concept has recently been described as "an area repeatedly traversed by an animal during a specified time period, with a boundary defined by proportion of occurrence" (Kenward, 2001). The underlying assumptions are that an area with high quality resources will be used more than one with low quality, that availability of or access to resources is not uniform, and that use of the home range may change with availability or time frame (Manly et al., 2002; Buskirk and Millsaugh, 2003). Hayne (1949) proposed the concept of "centers of activity" to identify areas of higher use within the larger area used. This term was replaced with the term "core area" (Kaufman, 1962) and implies the ability to distinguish between differential intensities of use by an animal. Techniques such as utilization distribution based approaches are particularly helpful in identifying differential use patterns. Behavioral activities can be grouped into those associated with relatively short-range movements within a consistent area or timeframe or with longer-range movements between areas or timeframes. Quantifying the area used, differences in areas used during different life history periods, and areas in which use is centered are fundamental approaches to understanding bat ecology and behavior (Kernohan, 2001).

A variety of methods have been used to estimate an animal's home range, including minimum convex polygon (Hayne, 1949), bivariate normal (Jennrich and Turner, 1969), and fixed and adaptive kernel (Silverman, 1986; Worton, 1989). Home range estimators can be categorized into (a) polygon, (b) grid cell, or (c) probabilistic methods. Home range estimators have been reviewed (Kenward, 1987; White and Garrott, 1990; Kernohan et al., 2001).

The accuracy and suitability of each home range estimator is affected by sampling design, including number of observations (Seaman et al., 1999), sampling scheme (Otis and White, 1999), and accuracy of locations (Anderson

Table 3.1. Comparison of home range estimators relative to requirements for sample size, distribution assumption, bias associated with small sample size, multiple centers of activity, use of utilization distributions, bias at inner and outer contours and sensitivity to outliers

Home Range Estimator Method	Estimator Type	Minimum Sample Size	Assumes Underlying Distribution	Relative Bias w/Small Sample Size	Allows for Multiple Centers of Activity	Includes Utilization Distribution	Performance at Inner Contours	Performance at Outer Contours	Sensitivity to Outliers
Minimum Convex Polygon	Non-parametric	>100	No	High	No	No	NA	NA	High
Bivariate Normal	Parametric	>20	Yes	Low	No	Yes	Good	Poor	Moderate
Harmonic Mean	Non-parametric	>70	No	High	Yes	Yes	Poor	Poor	Low
Fixed Kernel	Non-parametric	>30	No	Moderate	Yes	Yes	Moderate	Good	Low
Adaptive Kernel	Non-parametric	>30	No	Moderate	Yes	Yes	Good	Moderate	Low

et al., 2001). Selecting an estimator for home range analysis should consider biological considerations given the study design (e.g., whether assumptions of the method are met) and research objectives (Schoener, 1981). The sampling scheme should be compatible with the assumptions required by the home range estimator method selected. Fuller et al. (2005) offer a list of recommendations for selecting an appropriate space use estimator. A comparison of home range estimators is presented in Table 3.1.

Analysis Considerations

Sample Size

Radiotelemetry studies must take into account two measures of sample size: (1) the number of individuals tagged, and (2) the number and timing of relocations of each individual. An inherent limitation of all home range estimators and resource selection analysis is sampling error, which decreases with increasing sample size. Specific recommendations on sample sizes are difficult to make because of differences in animal use patterns, habitats that are available, and objectives of each study. Study designs that emphasize few bats with many locations for each bat can provide detailed knowledge for these particular bats, but they have limited application to a larger population. Such designs might be more applicable when the research population is small (e.g., endangered species), if the study objectives are focused on a few individuals or a specific area (e.g., a refuge), or if the study is designed to collect preliminary information on a relatively unknown population. Designs that emphasize the opposite extreme (many individuals with few locations per animal) also should be avoided. This design will not provide sufficient information to assess the habitat selection patterns of individual animals and how these patterns might vary among animals. Given that the appropriate sampling unit in re-

source selection studies is the individual (Aebischer et al., 1993; Otis and White, 1999), attempts to collect a truly representative sample of habitats used by an animal is more important. Explicit attention should be given to developing a sampling protocol that characterizes each time period of activity of interest. For example, many bat species will forage in familiar areas during early hours of the night, but it is fairly common for bats to make excursions of some distance from their usual locations; these may be just prior to night roosting or just prior to dawn. These movements may represent biological (i.e., exploration for new foraging or roosting areas) or methodological (i.e., improved telemetry methods that document previously undetectable movements) observations.

An additional consideration is seasonal shifts in use patterns. Although this may be of lesser concern due to the short life typical of small transmitters, considerable changes in use patterns have been documented between pregnancy, lactation, and postlactation periods (Racey, 1985; Rydell, 1989; Kurta et al., 1989; Feldhammer et al., 2001). When comparing between animals or studies, timing and intensity of data collected should be comparable.

Several researchers have focused on the question of the number of animals versus the number of locations to collect using simulation approaches. Alldredge and Ratti (1986) compared habitat selection analyses for different numbers of animals, locations per animal, and number of habitat types available. They observed that several methods work well when the number of habitats is small (e.g., five types), more than 20 animals are used, and 50 locations per animal are obtained. In general, as the number of animals or the number of observations increases, the test is more powerful in detecting differences between habitat use and availability. They recommended against having few observations (e.g., 15) on few animals (<20),

because this design can easily result in the conclusion that no habitat selection is occurring. Similarly, Leban et al. (2001) evaluated sample size effects on compositional analysis, and Neu et al. (1974) evaluated six resource features (aspect, distance to cover, forage, open roads, percent canopy closure, and vegetation types) using field data. They reported that increasing the number of observations had little influence on compositional analysis results. Their suggestions paralleled Alldredge and Ratti (1986) in that a minimum of 20 animals with 50 observations each is needed to estimate resource selection during the period of interest (i.e., season). Nevertheless, meaningful results can often be obtained with 30 locations each from 10–20 animals if selection effects are reasonably strong, as in the original demonstration of compositional analysis (Aebischer et al., 1993). Alldredge and Ratti (1986) further concluded that Type I and Type II error rates should be considered in selecting sample sizes when habitat selection studies are planned.

Some home range estimators are based on assumptions about the distribution of data. The accuracy of all home range estimators depends on sample size. Since animal distribution within an area during a specific time period rarely conforms to a simple statistical distribution, sample sizes required to accurately assess home ranges also vary. For kernel-based estimates of home range size, Seaman et al. (1999) suggested 30 (and preferably 50) locations per animal be used. Unlike other estimators, Seaman et al. (1999) found that adaptive kernel methods are overestimated with fewer than 30 locations. With other estimators, such as the minimum convex polygon, increasing sample sizes results in increased home range sizes (Kernohan et al., 2001).

Analysis Software

A number of analytical methods are available to estimate an animal's position based on triangulation methods. White and Garrott (1990) provide SAS/FORTAN programs for estimating an animal's location from triangulation techniques. Software packages that link these programs to a database and digital maps have also been developed. For example, GTM (Sartwell, 2003) is a Windows-based system that imports and incorporates geographic information coverages (GIS) from a wide variety of spatial data formats: ArcView, MapInfo Vector, AutoCad DWG, TIFF Image, and Windows BMP. Telemetry azimuths, animal sightings, and internally generated location or home range estimates are then stored graphically as data overlay layers on top of the base map(s). A variety of coordinate systems is supported, and coordinate conversion is available. The software is designed for real-time field use on laptops or portable computers. Location estimators currently include maximum likelihood estimators (MLE), Huber m-estimators, and Andrews m-estimators. Information on available software is included in Appendix 3.2.

Analysis of Resource Use

Resource selection is a hierarchical process of behavioral responses that result in differential use of habitats (Block and Brennan, 1993). Radiotelemetry locations or visual observations of locations involved with the animals' daily pursuit of its environmental needs are referred to as "used" resources. Specific environmental and habitat covariates can be associated with these resources. "Selected" resources are used more often than their availability, and "avoided" resources are those used less often than their availability in the environment. Resource "preference" refers to situations when an animal has equal access to all available resources, such as in a controlled experiment, to determine those preferentially selected if offered on an equal basis.

Four designs for resource selection studies have been identified (Thomas and Taylor, 1990; Manly et al., 2002), based on level of resource use (population or individual animal) and measures of resource availability. Design 1 studies determine use at the population level, with available, used, or unused resource units sampled or censused for the study area or to encompass all animals. This design assumes a relationship between density and relative preference, an assumption that is violated if detectability of animals varies among habitats, which is commonly the case for bat species that use both open and heavily forested habitats (Thomas and Taylor, 1990). Design 2 studies determine use by individual animals, but availability is measured at the population level. Design 3 also identifies individuals, but both used and available (or used and unused) resources are sampled or censused for each animal. Design 4 identifies individuals with availability defined for every location (Erickson et al., 2001). Inferences about selection are made at the population level within the study area in designs 1 and 2, whereas designs 3 and 4 make inferences about selection within home ranges or feeding sites (Thomas and Taylor, 1990). Aggregating results across many animals studied under design 3 can result in population-level inferences about the variability of third-order selection among individuals.

Habitat selection may occur at four levels: (1) the species' physical or geographic range, (2) the individual home ranges within the geographic range (3) the use of features within its home range, or (4) for particular elements such as food items (Johnson, 1980). Patterns of resource selection may be scale dependent if the value of the resources to animals in terms of promoting long-term reproductive fitness differs between levels (Rettie and Messier, 2000). This hierarchical process of resource selection necessitates that an investigator carefully consider which scale(s) to study resource selection. Although multiple scales are often studied, explicit consideration of scale is critical because that defines inferences from the study and identifies key features such as experimental units.

The concept and quantification of resource availability is central to most resource selection studies. Because resource selection studies have traditionally compared used resources to available resources, the scale and context of what is defined as "available" to an animal is ultimately important. Determination of availability should be matched to the appropriate scale of the analysis and the behavioral characteristics of the animal under study. Buskirk and Millsaugh (2006) reviewed the nuances and techniques to define available habitats.

Accurate determination of habitat use (e.g., animal location) is an underlying assumption of most analysis programs. Errors in tracking (e.g., triangulation) or observation (e.g., incorrectly marking the location on a map) can bias studies on resource selection (Nams, 1989; White and Garrott, 1990; Samuel and Kenow, 1992; Rettie and McLoughlin, 1999). Errors in classification of habitat use will result in incorrect rankings or reduce the power of statistical tests for habitat selection (White and Garrott, 1986; Nams, 1989). Some researchers have directly considered use as the general area surrounding the location estimate (Rettie and McLoughlin, 1999). When telemetry error is large relative to patch size, this approach may be appropriate. Samuel and Kenow (1992) proposed a method to account for telemetry error for habitat selection tests by using the error distribution of each animal location to assess habitat misclassification. Buskirk and Millsaugh (2006) discuss other currencies of use, such as distance traveled, and the inherent advantages and disadvantages of each.

Numerous analytical methods have been developed for analyzing resource use data. These include univariate methods such as chi-square goodness of fit (Neu et al., 1974), rank-order tests (Johnson, 1980); and compositional analysis (Aebischer et al., 1993), as well as multivariate methods including logistic regression (Thomasma et al., 1991), polytomous logistic regression (North and Reynolds, 1996), and discrete choice (Cooper and Millsaugh, 1999). Each of these methods has strengths and weaknesses that range from appropriate identification of the experimental unit to accuracy of point estimates. Alldredge et al. (1998) reviewed methods of resource selection and concluded studies that characterize locations seem to require logistic regression, or more generally, resource selection functions (Manly et al., 1993), in which the probability of a resource unit being used is proportionate to the value of characteristics measured for the unit. Resource selection functions provide a model-based approach that is preferable to previously used ad hoc methods (Alldredge et al., 1998) and are determined by various analysis methods from simple univariate rankings to more complex multivariate approaches (Fig. 3.4).

The Neu et al. (1974) method uses a chi-square goodness-of-fit analysis to determine whether resource use equals resource availability. A significant chi-square test indicates a difference in use and availability; these differences

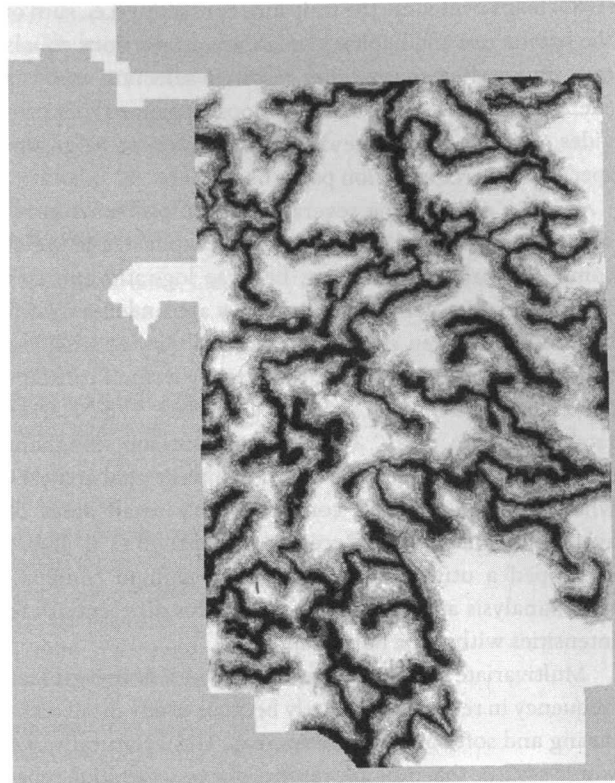


Figure 3.4. Resource selection function calculated for elk in South Dakota. From Millsaugh et al., 2006.

can be investigated using confidence intervals on the difference in percent use and percent availability (Byers et al., 1984; Cherry, 1996). The goodness-of-fit test assumes that habitat availability is measured without error, which is problematic in light of issues identified above. The technique also assumes that all observations of habitat use are independent, which is problematic when multiple animals are relocated together (e.g., bats foraging in the same general location). Ignoring this assumption inflates Type I error rates. Dasgupta and Alldredge (1998) suggested a method to incorporate data on dependent behavior of radio-tagged animals into the chi-square framework. Thus, they alleviate the need to count multiple animal observations at one location as one (Alldredge and Ratti, 1986, 1992).

Aebischer et al. (1993) were the first to propose use of compositional analysis, a multivariate analysis of variance, for studies of wildlife habitat selection. Compositional analysis helps overcome several common problems in wildlife studies (Aebischer et al., 1993; Pendleton et al., 1998), and for this reason it has become a popular technique (e.g., McLellan and Hovey, 2001; Morrison and Humphrey, 2001). In compositional analysis, the animal, not the individual location points, are the experimental unit. This helps overcome problems of unequal weighting among animals when the number of locations across animals is not equal (Pendleton et al., 1998). The log-ratio transformation used in compositional analyses Aitchison

(1986) helps overcome the unit sum constraint (i.e., sum of the habitat use and habitat availability proportions equals one) imposed on many other resource selection analyses (Aebischer et al., 1993). Last, compositional analysis provides a mechanism for evaluating differences in group-specific resource selection patterns.

Despite overcoming several common problems in resource selection studies, a few issues complicate the use of compositional analysis. First, because log-ratio analyses do not allow for zeroes (because they are undefined), difficulties arise when either use or availability of a habitat type is nil. Often, zeroes are replaced by a small constant (Aebischer et al., 1993), which can inflate Type I error rates (Bingham et al., 2004). For this reason, Bingham et al. (2004) questioned the use of compositional analyses when habitat categories contained very small areas of availability and 0% use. Recently, Millspaugh et al. (2006) developed a utilization distribution weighted compositional analysis approach that accounts for differential use intensities within the home range.

Multivariate methods have also been used with greater frequency in recent years, partly because of advanced computing and software capabilities (e.g., GIS). Naturally, we would assume that multiple resources (e.g., vegetation type, distance to roads and water, elevation) could influence animal resource selection. Thus, many researchers have considered multivariate procedures that allow insight into various interacting categorical and continuous types of resource data. Manly et al. (2002), Millspaugh and Marzluff (2001), and other sources, such as special sections in the *Journal of Wildlife Management* (forthcoming) and the *Journal of Agricultural, Biological, and Environmental Statistics* (1998), have reviewed multivariate procedures for analysis of resource selection by animals. With recent advancements in GIS technology and supporting software to compute landscape metrics, the potential number of covariates is large. The number of possible factors to consider must be carefully selected based upon the objectives of the study, hypotheses to be tested, limitations of location data, available resource information, and most importantly, consideration of the ecology and behavior of the animal. The principle of parsimony suggests that a model should have "the smallest possible number of parameters for adequate representation of the data" (Box and Jenkins, 1970, p. 17). Burnham and Anderson (2002) offer some useful advice in selecting covariates and candidate models. They recommend the painful exercise of thinking about the objective of the modeling exercise and model alternatives prior to collecting or analyzing the data. For many resource selection studies, the procedure of developing these a priori models to test specific hypotheses may help advance our understanding of bat and habitat relationships. There is adequate information for many bat species that allows the development of good testable candidate models.

Traditional binary logistic regression has become a popular technique to compare resources at used and available sites due in part to its availability in standard statistical packages and exploratory power (Manly et al., 2002). Logistic regression differs from linear regression in that the former uses a binary response variable. Often, relocation points define the used resources and random points within the home range or study area define available points, although variations exist (Compton et al., 2002; Manly et al., 2002). The technique is useful because it relates the response variable (used or available, or presence or absence) to one or more independent variables that are of interest. The resulting resource selection function (Manly et al., 2002) estimates the probability the site will be used by the animal as a function of important resource variables or a priori models derived through the analysis process. However, "available" locations may actually be "used" points meaning that the sample of available locations may contain observations of both used and unused sites, which causes difficulty in interpreting results of use versus availability (Keating and Cherry, 2004). In addition, there are concerns using this procedure when telemetry error is high because features are measured at relocation points (e.g., distance to water, habitat at site).

Using polytomous or multinomial logistic regression to assess resource selection was first proposed by North and Reynolds (1996). In contrast to traditional binary logistic regression, which relies on used and available resources, the polytomous logistic procedure (North and Reynolds, 1996) does not compare the characteristics of used to available sites. Instead, characteristics of varying use-intensity sites (e.g., low, medium, and high patches) are compared to determine those resources that most differentiate among use sites. In other words, it models the probability that site belongs to a use-intensity group as a function of important resource characteristics. Because the procedure does not consider areas where locations were not observed, it only considers used locations, which might be beneficial when trying to quantify resource availability (North and Reynolds, 1996).

Use of discrete choice modeling, a common technique in the economics literature (Ben-Akiva and Lerman, 1985), was proposed by Cooper and Millspaugh (1999, 2001) to study wildlife resource selection. Arthur et al. (1996) used a similar approach when evaluating habitat use by polar bears. The data necessary to estimate the multinomial logit form of the discrete choice model are similar to data required for the standard logistic regression model described above (Cooper and Millspaugh, 1999). The main benefit of discrete choice is that the researcher has maximum flexibility in defining resource availability. Although it compares used to available sites, as with traditional binary logistic regression, discrete choice allows the investigator to pair used with available sites. In this way, discrete choice can be thought of as a "case control" design be-

cause each point of use is paired with one or several points of availability. This procedure is particularly beneficial when an investigator has data observations over short periods of time, when restricting what was available to the animal is necessary. The technique would also be helpful in investigations of bat roosting locations because one controls the pairing of used and available points, making it more certain that what was selected as available was truly available to the animal.

FUTURE DIRECTIONS FOR RADIOTELEMETRY STUDIES

Radiotelemetry has become an important tool in many modern studies of bat behavior, ecology, management, and conservation because of the dramatic increases in our technological capabilities to locate these animals. The development of new approaches to data analysis has dramatically improved our ability to evaluate and estimate bat home range requirements and habitat selection. Studies using radiotelemetry will continue to improve substantially through increased knowledge of the powerful statistical tools that have been developed for this kind of data as well as how to apply basic principles of finite population sampling.

Telemetry technology is rapidly advancing; therefore, bat researchers should identify their study objectives clearly and define their scope of inference, then carefully consider whether radiotelemetry is an appropriate or feasible method. Factors such as impacts from transmitter attachment should not be ignored. Selection of analysis methods for home range and habitat use data will depend on the type and accuracy of data collected, assumptions and limitations of the selected sampling and analysis method, and the hypothesis to be tested. The analysis and application of telemetry data has benefited greatly from recent advances in computing software and other technologies (e.g., GPS). These advancements have sparked the development of several new analytical techniques to address long-standing questions of bat ecology.

In this chapter, we have outlined considerations for designing and implementing a bat radiotelemetry study, as well as general advantages and disadvantages of analytical procedures with the hope that this information will help guide future bat researchers toward the goals of understanding and conserving these amazing and beneficial mammals.

APPENDIX 3.1

Sources of Radiotelemetry Equipment

Advanced Telemetry Systems, Inc.
470 First Ave. N.
Box 398
Isanti, MN 55040, USA
Phone: 763-444-9267

Fax: 763-444-9384
E-mail: 70743.512@compuserve.com
Website: www.atstrack.com

American Wildlife Enterprises
737 Silver Lake Road
Monticello, FL 32344, USA
Phone: 850-997-3551
Fax: 850-997-3552

Austec Electronics, Ltd.
#1006, 11025-82 Ave.
Edmonton, Alberta KT6G 0T1
Canada
Phone: 403-432-1878
Fax: 415-449-3980

AVM Instrument Company, Ltd.
PO Box 1898
1213 South Auburn Street
Colfax, CA 95713, USA
Phone: 530-346-6300
Fax: 530-346-6306
Website: www.avminstrument.com/
(Radiotelemetry instrumentation)

Biotelemetry, Inc.
6520 Contempo Lane
Boca Raton, FL 33433, USA
Phone: 561-394-0315
Fax: 561-394-0315
(Micro-miniature implantable transmitters)

Bio Telemetry Tracking
18 Magill Rd
Norwood, SA 5067
Australia
Phone: +61-8-8362-6666
Fax: +61-8-8362-7955
(Distributor of receivers made by Yaesu, of Japan)

Biotrack Ltd.
52 Furzebrook Rd.
Wareham Dorset BH20 5AX
United Kingdom
Phone: +44(0) 1929 552 992
Fax: +44(0) 1929 554 948
Website: www.biotrack.co.uk
(Telemetry systems and software)

Blackburn Transmitters
819 Logansport Street
Nacogdoches, TX 75961, USA
Phone: 936-560-3360
Fax: 936-569-2009
E-mail: pblackburn@cox-internet.com
(Radio transmitters; specializing in custom-built, very small transmitters)

BlueSky Telemetry Ltd.
PO Box 7500
Aberfeldy
Scotland, PH15 2YG
United Kingdom
Phone: +44(0) 1887 820 816
Fax: +44(0) 1887 820 979

Website: www.blueskytelemetry.com
(GPS wildlife telemetry collars and tags)

Christensen Designs
349 Scenic Place
Manteca, CA 95337, USA
Phone: 800-928-9111 / 209-239-8090
Fax: 209-239-5414

Website: www.PeeperPeople.com
(Video and surveillance systems for nests and burrows)

Custom Electronics of Urbana, Inc.
2009 Silver Ct. W.
Urbana, IL 61801, USA
Phone: 217-344-3460
Fax: 217-344-3460
E-mail: BSZELPAL@aol.com
(Receivers and antennas)

Custom Telemetry Co.
1050 Industrial Drive
Watkinsville, GA 30677, USA
Phone: 706-769-4024
Fax: 706-769-4026

Data Sciences International, Inc.
119 14th Street NW
St. Paul, MN 55112, USA
Phone: 651-481-7400 / 800-262-9687 (U.S. and Canada)
Fax: 651-481-7417
E-mail: information@datasci.com
Website: www.datasci.com
(Physiological telemetry)

Holohil Systems Ltd.
112 John Cavanaugh Drive
Carp, Ontario K0A 1L0
Canada
Phone: 613-839-0676
Fax: 613-839-0675
E-mail: info@holohil.com
Website: www.holohil.com
(Radio transmitters)

Johnson's Telemetry
Route 4, Box 313
El Dorado Springs, MO 64744, USA
Phone: 417-876-5083

KVH Headquarters
50 Enterprise Center
Middletown, RI 02842-5279, USA
Phone: 401-847-3327
Fax: 401-849-0045
(Electronic compass engine)

L. L. Electronics
P.O. Box 420#2, Pearl Dr.
Mahomet, IL 61853, USA
Phone: 215-586-5327, 800-553-5328

Lotek Wireless, Inc.
114 Cabot Street
St. John's, Newfoundland A1C 1Z8
Canada
Phone: 709-726-3899
Fax: 709-726-5324

E-mail: marine.telemetry@lotek.com
Website: www.lotek.com

Mariner Radar Ltd.
Bridleway, Campsheath
Lowestoft, Suffolk NR32 5DN
England
Phone: 44-1502-567-195
Fax: 44-1502-567-762
(Transmitters used with satellites)

Merlin Systems, Inc.
445 W Ustick Rd
Meridian, ID 83642, USA
Phone: 208-884-3308
Fax: 208-888-9528
E-mail: merlin@cyberhighway.net

Microwave Telemetry, Inc.
6214 Satanwood Drive
Columbia, MD 21044, USA
Phone: 301-964-2687
Fax: 301-964-0816
(General and satellite)

Philips Respirationics
20300 Empire Avenue
Building B-3
Bend, OR 97701, USA
Phone: 800-685-2999 (U.S., Canada, and Mexico)
Phone: 541-598-3800 (Worldwide)
Fax: 541-322-7277
Email: mm@respirationics.com
Website: www.minimitter.com
(Physiological telemetry)

Nature Conservation Bureau Ltd
36 Kingfisher Court
Hambridge Road
Newbury RG14 5SJ
United Kingdom
Phone: +44 1635 550380
Fax: +44 1635 550230
E-mail: 100347.1526@compuserve.com

North Star Science and Technology, LLC
P.O. Box 438
King George, VA 22485, USA
Phone: 410-961-6692; 540-775-4698
Fax: 603-462-5144
Website: www.northstarst.com
(Satellite-based telemetry)

Service Argos
18, Avenue Edouard Belin
31055 Toulouse Cedex, France
61-39-4799
and
1801 McCormick Dr., Suite 10
Landover, MD 20785, USA
Phone: 301-925-4411
Fax: 301-925-8995
E-mail: jw@argosinc.com
Website: www.argosinc.com
(Satellite system)

Sirtrack Limited
 Private Bag 1403
 Goddard Lane
 Havelock North 4157
 New Zealand
 Phone: +64 6 877 7736
 Fax: +64 6 877 5422
 E-mail: name@sirtrack.com
 Website: www.sirtrack.com
 (Designs, builds, and packages radio tracking and telemetry equipment for wildlife research)

Smith-Root, Inc.
 14014 Northeast Salmon Creek Ave.
 Vancouver, WA 98686, USA
 Phone: 206-573-0202
 Fax: 503-286-1931
 (Aquatic radio telemetry)

Sonotronics
 1130 E. Pennsylvania St.
 Suite 505
 Tucson, AZ 85714, USA
 Phone: 520-746-3322
 Fax: 520-294-2040
 E-mail: mgregor@azstarnet.com
 Website: www.media-masters.com/sonotronics

Telemetry Solutions
 1130 Burnett Ave., Suite J
 Concord, CA 94520, USA
 Phone: 925-798-2373
 Fax: 925-798-2375
 E-mail: qkermeeen@telemetrysolutions.com
 Website: www.telemetrysolutions.com

Telemetry Systems, Inc.
 P.O. Box 187
 Mequon, WI 53092, USA
 Phone: 414-241-8335

Televilt International AB
 Box 53
 S-711 22 Lindesberg
 Sweden
 Phone : +46-581-17195
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 E-mail: per-arne.lemnell@televilt.se
 Website: www.televilt.se

Telonics, Inc.
 932 Impala Ave.
 Mesa, AZ 85204-6699, USA
 Phone: 602-892-4444
 Fax: 602-892-9139
 E-mail: info@telonics.com
 Website: www.telonics.com
 (General and satellite telemetry)

Titley Electronics Pty Ltd
 P.O. Box 19
 Ballina, NSW 2478

Australia
 Phone: +61 2-66-811-017
 Fax: +61 2-66-866-617
 E-mail: titley@nor.com.au
 Website: www.titley.com.au
 (Radio telemetry equipment; Anabat bat detectors)

Toyocom
 20-4, Nishi-Shimbashi 3-chome,
 Minato-ku, Tokyo 105
 Japan
 Phone: 03 -3459-7320
 Fax: 03 3436 1434
 and
 Chicago, IL, USA
 Phone: 708-593-8780
 Fax: 708-593-5678
 and
 Los Angeles, CA, USA
 Phone: 714-668-9081
 Fax: 714-668-9158
 (Satellite telemetry)

Vemco
 211 Horseshoe Lake Drive
 Halifax, Nova Scotia B3S 0S9
 Canada
 Phone: 902-450-1700
 Fax: 902-450-1704
 E-mail: VEMCO Sales
 Website: www.vemco.com
 (Ultrasonic tags for aquatic animals)

Wildlife Computers
 8345 154th Avenue NE
 Redmond, WA 98052, USA
 Phone: 425-881-3048
 Fax: 425-881-3405
 E-mail: tags@wildlifecomputers.com
 www.wildlifecomputers.com
 (Time-data and satellite-linked recorders with software)

Wildlife Materials, Inc.
 Route 1, Box 427A
 Carbondale, IL 62901, USA
 Phone: 618-549-6330 / 618-549-2242
 Fax: 618-457-3340
 E-mail: wmi@midwest.net
 Website: www.wildlifematerials.com

Wildlink Inc.
 2924 98th Avenue, North
 Brooklyn Park, MN 55444, USA
 Voice/fax: 612-424-8340 / 800-421-8340
 (Large mammal data acquisition and recapture)

Ziboni Ornitecnica, s.r.l.
 Costa Volpino (Bergamo)
 Italy
 Phone: 035-970434
 Fax: 035-972488

APPENDIX 3.2

Sources of Software for Radiotelemetry Analysis

Package Name	Reference	Non/Parametric Techniques	Author	Description
CALHOME	J. Kie	Both	J. Kie	Pick from many home range analysis methods: minimum convex polygon, bivariate normal, harmonic mean, and adaptive kernel. http://nhsbig.inhs.uiuc.edu/wes/home_range.html
DIXON	Dixon and Chapman, 1980	Nonparametric	Dixon and Chapman	Dixon uses a harmonic mean analysis as its method of finding the home range of an animal. It requires a math coprocessor.
ESRI	www.esri.com/	Both	P.N. Hooze and B. Eichenlaub ASCE, USGS	Animal Movement is an ArcView extension that contains a collection of over 40 functions specifically designed to aid in the analysis of animal movement. www.absc.usgs.gov/giba/
FRAGSTATS	McGarigal and Marks, 1994	N/A	Kevin McGarigal, Barbara Marks	Fragstats quantifies landscape structure through numerous metrics including area, patch density, size, and variability metrics; edge, shape, core area, and diversity metrics; and contagion and interspersal metrics. A vector image and raster image version are available. The raster version also computes several nearest neighbor metrics. www.umass.edu/landeco/research/fragstats/fragstats.html
HOMERANGE	Ackerman et al., 1990	Both	Robert Huber, Jack Bradbury	HomeRange is primarily for use in the analysis of spatial data in animal behavior. E. O. Garton Forestry, Wildlife and Range Exp. Stn. University of Idaho Moscow, Idaho 83843
KERNELHR	Seaman and Powell, 1991	Nonparametric	Erran Seaman	KERNELHR performs kernel-based estimates of two-dimensional (bivariate) data. Works well for any two-dimensional data. Users may select between output of density and utilization distribution, change the size of the smoothing parameter and grid, and output values at the observation or on a grid. http://fwie.fw.vt.edu/
McPAAL	Stüwe and Blohowiak, 1985	Both	Michael Stüwe	
RANGES VIII	Kenward, 1990	Nonparametric		(V) www.ceh.ac.uk (VI) www.anatrack.com

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LITERATURE CITED

- Aebischer, N. J., P. A. Robertson, and R. E. Kenward. 1993. Compositional analysis of habitat use from animal radio tracking data. *Ecology* 74: 1313-1325.
- Aitchison J., 1986. *The Statistical Analysis of Compositional Data*. Chapman & Hall, London.
- Aldridge, H. D. J. N., and R. M. Brigham. 1988. Load carrying and maneuverability in an insectivorous bat: a test of the 5% "rule" of radio-telemetry. *Journal of Mammalogy* 69: 379-382.
- Allredge, J. R., and J. T. Ratti. 1986. Comparison of some statistical techniques for analysis of resource selection. *Journal of Wildlife Management* 50: 157-165.
- . 1992. Further comparison of some statistical techniques for analysis of resource selection. *Journal of Wildlife Management* 56: 1-9.
- Allredge, J. R., D. L. Thomas, and L. L. McDonald. 1998. Survey and comparison of methods for study or resource selection. *Journal of Agricultural, Biological, and Environmental Statistics* 3: 237-253.
- Amelon, S. K., F. R. Thompson, K. Heun, and J. Amelon. 2003. Use of a portable radiotelemetry tower and vehicular system for radiotracking *Lasiurus borealis*, *Myotis septentrionalis* and *Myotis grisescens* in Missouri. *Bat Research News* 44: 19.

- American Society of Mammalogists. 1998. Guidelines for the capture, handling and care of mammals. *Journal of Mammalogy* 79: 1416–1431.
- Amlaner, C. J., and D. W. MacDonald (eds.). 1980. *A Handbook on Biotelemetry and Radio Tracking*. Pergamon Press, Oxford.
- Anderka, F. W. 1987. Radiotelemetry techniques for furbearers. Pages 216–227. In: *Wild Furbearer Management and Conservation in North America* (M. Novak, J. A. Baker, M. E. Obbard, and B. Malloch, eds.). Ontario Ministry of Natural Resources, Toronto, Canada.
- Anderson, D. R., W. A. Link, K. P. Burnham, and D. H. Johnson. 2001. Suggestions for presenting the results of data analysis. *Journal Wildlife Management* 65: 373–378.
- Arthur, S. M., B. F. J. Manly, L. L. McDonald, and G. W. Garner. 1996. Assessing habitat selection when availability changes. *Ecology* 77: 215–227.
- Banks, E. M., R. J. Brooks, and J. Schnell. 1975. A radiotracking study of home range and activity of the brown lemming (*Lemmus trimucronatus*). *Journal of Mammalogy* 56: 888–901.
- Barclay, R. M. R., M. C. Kalcounis, C. Stefan, L. H. Crampton, M. J. Vonhof, and L. Wilkinson. 1996. Can external radiotransmitters be used to assess body temperature and torpor in bats? *Journal of Mammalogy* 77: 1102–1106.
- Ben-Akiva, M., and S. R. Lerman. 1985. *Discrete Choice Analysis: Theory and Application to Travel Demand*. MIT Press, Cambridge, Massachusetts.
- Bingham, R. L., and L. A. Brennan. 2004. Comparison of Type I error rates for statistical analysis of resource selection. *Journal of Wildlife Management* 68: 206–212.
- Block, W. M., and L. A. Brennan. 1993. The habitat concept in ornithology: theory and applications. Pp. 35–91. In: *Current Ornithology* (D. M. Power, ed.). Plenum Press, New York.
- Bontadina, F., H. Schofield, B. B. F. Naef-Daenzer, H. Schofield, and B. Naef-Daenzer. 2002. Radio-tracking reveals that lesser horseshoe bats (*Rhinolophus hipposideros*) forage in woodland. *Journal of Zoology (London)* 258: 281–290.
- Box, G. E. P., and G. M. Jenkins. 1970. *Time Series Analysis*. Holden-Day, San Francisco.
- Brigham, R. M., M. J. Vonhof, R. M. R. Barclay, and J. C. Gwilliam. 1997. Roosting behavior and roost-site preferences of forest-dwelling California bats (*Myotis californicus*). *Journal of Mammalogy* 78: 1231–1239.
- Burnham, K. P., and D. R. Anderson. 2002. *Model Selection and Multimodel Inference: A Practical Information-theoretic Approach*. Springer-Verlag, New York.
- Burt, W. H. 1943. Territoriality and home range concepts as applied to mammals. *Journal of Mammalogy* 24: 346–352.
- Buskirk, S. W., and J. J. Millspaugh. 2003. Defining availability and selecting currencies of use: key steps in modeling resource selection. Pp. 1–11. In: *Resource Selection Methods and Applications* (S. Huzurbazar, ed.). Proceedings of the First International Conference on Resource Selection, Laramie, Wyoming. Omnipress, Madison, Wisconsin, and Western EcoSystems Technologies, Cheyenne, Wyoming.
- . 2006. Metrics for studies of resource selection. *Journal of Wildlife Management* 70: 358–366.
- Byers, C. R., R. K. Steinhorst, and P. R. Krausman. 1984. Clarification of a technique for analysis of utilization: availability data. *Journal of Wildlife Management* 48: 1050–1053.
- Cederlund, G., and P. A. Lemnell. 1980. A simplified technique for mobile radio tracking. Pp. 319–322. In: *A Handbook on Biotelemetry and Radio Tracking* (C. J. Amlaner and D. W. Macdonald, eds.). Pergamon Press, Oxford.
- Cherry, S. 1996. A comparison of confidence interval methods for habitat use-availability studies. *Journal of Wildlife Management* 60: 653–658.
- Compton, B. W., J. M. Rhymer, and M. McCollough. 2002. Habitat selection by wood turtles (*Clemmys insculpta*): an application of paired logistic regression. *Ecology* 83: 833–843.
- Cooper, A. B., and J. J. Millspaugh. 1999. The application of discrete choice models to wildlife resource selection studies. *Ecology* 80: 566–575.
- . 2001. *Radio Tracking and Animal Populations*. Academic Press, San Francisco.
- Dasgupta, N., and J. R. Alldredge. 1998. A multivariate X^2 analysis of resource selection data. *Journal of Agricultural, Biological, and Environmental Statistics* 3: 323–334.
- Dixon, K. R., and J. A. Chapman. 1980. Harmonic mean measure of animal activity areas. *Ecology* 61: 1040–1044.
- Erickson, W. P., T. L. McDonald, K. G. Gerow, S. Howlin, and J. W. Kern. 2001. Statistical issues in resource selection studied with radio-marked animals. Pp. 211–242. In: *Radio Tracking and Animal Populations* (J. J. Millspaugh and J. M. Marzluff, eds.). Academic Press, San Diego.
- Feldhammer, G. A., T. C. Carter, and S. K. Carroll. 2001. Timing of pregnancy, lactation and female foraging activity in three species of bats in southern Illinois. *Canadian Field-Naturalist* 115: 420–424.
- Focardi, S., P. Marcellini, and P. Montanaro. 1996. Do ungulates exhibit a food density threshold? A field study of optimal foraging and movement patterns. *Journal of Animal Ecology* 65: 606–620.
- Fuller, M. R., J. J. Millspaugh, K. E. Church, and R. E. Kenward. 2005. *Wildlife radiotelemetry*. Pp. 377–417. In: *Research and Management Techniques for Wildlife and Habitats* (T. A. Bookhout, ed.). The Wildlife Society, Bethesda, Maryland.
- Garton, E. O., M. J. Wisdom, F. A. Leban, and B. K. Johnson. 2001. Experimental design for radiotelemetry studies. Pp. 1–42. In: *Radio Tracking and Animal Populations* (J. J. Millspaugh and J. M. Marzluff, eds.). Academic Press, San Diego.
- Hayne, D. W. 1949. Calculation of size of home range. *Journal of Mammalogy* 30: 1–18.
- Hayssen, V., and T. H. Kunz. 1996. Allometry of litter mass in bats: comparisons with respect to maternal size, wing morphology, and phylogeny. *Journal of Mammalogy* 77: 476–490.
- Henry, M., D. W. Thomas, R. Vaudry, and M. Carrier. 2002. Foraging distances and home range of pregnant and lactating little brown bats (*Myotis lucifugus*). *Journal of Mammalogy* 83: 767–774.
- Hickey, M. B. C. 1992. Effect of radiotransmitters on the attack success of hoary bats, *Lasiurus cinereus*. *Journal of Mammalogy* 73: 344–346.
- Hicks, A., K. C. Swartz, G. M. Greene, and S. von Oettingen. 2002. Improvements in using aircraft to track Indiana bats, *Myotis sodalis*, from their hibernacula to summer range. *Bat Research News* 43: 150.

- Jennrich, R. I., and F. B. Turner. 1969. Measurement of a non-circular home range. *Journal of Theoretical Biology* 22: 227–237.
- Johnson, D. H. 1980. The comparison of usage and availability measurements for evaluating resource preference. *Ecology* 61: 65–71.
- Kalko, E. K. V., D. Friemel, C. O. Handley, Jr., and H.-U. Schnitzler. 1999. Roosting and foraging behavior of two neotropical gleaner bats, *Tonatia silvicola* and *Trachops cirrhosus* (Phyllostomidae). *Biotropica* 31: 344–353.
- Kaufman, J. H. 1962. Ecology and social behavior of the coati, *Nasua narica* on Barro Colorado Island Panama. University of California Publications in Zoology 60: 95–222.
- Keating, K., and S. Cherry. 2004. Use and interpretation of logistic regression in habitat-selection studies. *Journal of Wildlife Management* 68: 774–789.
- Kenward, R. E. 1987. *Wildlife Radio Tagging: Equipment, Field Techniques and Data Analysis*. Academic Press, London.
- . 2001. *A Manual for Wildlife Radio Tagging*. Academic Press, London.
- Kernohan, B. J., R. A. Gitzel, and J. J. Millspaugh. 2001. Analysis of animal space use and movements. Pp. 126–164. In: *Radio Tracking and Animal Populations* (J. J. Millspaugh and J. M. Marzluff, eds.). Academic Press, San Diego.
- Kerth, G., M. Wagner, and B. König. 2001. Roosting together, foraging apart: information transfer about food is unlikely to explain sociality in female Bechstein's Bats (*Myotis bechsteinii*). *Behavioral Ecology and Sociobiology* 50: 283–291.
- Kurta, A., and S. W. Murray. 2002. Philopatry and migration of banded Indiana bats (*Myotis sodalis*) and effects of radio transmitters. *Journal of Mammalogy* 83: 585–589.
- Kurta, A., G. P. Bell, K. A. Nagy, and T. H. Kunz. 1989. Energetics of pregnancy and lactation in free-ranging little brown bats (*Myotis lucifugus*). *Physiological Zoology* 62: 804–818.
- Lacki, M. J., and J. H. Schwieterjohann. 2001. Day-roost characteristics of northern bats in mixed mesophytic forest. *Journal of Wildlife Management* 65: 482–488.
- Lacki, M. J., S. K. Amelon, and M. D. Baker. 2007. Foraging ecology of bats in forests. Pp. 83–128. In: *Bats in Forests: Conservation and Management* (M. J. Lacki, J. P. Hayes, and A. Kurta, eds.). Johns Hopkins University Press, Baltimore, Maryland.
- Law B. S., and M. Lean. 1999. Common blossom bats (*Syconycteris australis*) as pollinators in fragmented Australian tropical rainforest: a comparative study of two lowland tropical plants. *Biological Conservation* 91: 201–212.
- Leban, F. A., M. J. Wisdom, E. O. Garton, B. K. Johnson, and J. G. Kie. 2001. Effect of sample size on the performance of resource selection analyses. Pp. 291–307. In: *Radio Tracking and Animal Populations* (J. J. Millspaugh and J. M. Marzluff, eds.). Academic Press, San Diego.
- Manly, B. F., L. L. McDonald, and D. L. Thomas. 1993. *Resource Selection by Animals: Statistical Design and Analysis of Field Studies*. Chapman & Hall, London.
- Manly, B. F., L. L. McDonald, D. L. Thomas, T. L. McDonald, and W. P. Erickson. 2002. *Resource Selection by Animals: Statistical Design and Analysis for Field Studies*. Kluwer Academic Publishers, Dordrecht, Netherlands.
- Matthews, P. A. 1965. *Radio Wave Propagation VHF and Above*. Chapman & Hall, London.
- McCulloch, C. E., and M. L. Cain. 1989. Analyzing discrete movement data as a correlated random walk. *Ecology* 70: 383–388.
- McGarigal, K., and B. J. Marks. 1994. *FRAGSTATS: Spatial Pattern Analysis Program for Quantifying Landscape Structure*. Version 2.0.
- McLellan, B. N., and F. W. Hovey. 2001. Habitats selected by grizzly bears in a multiple use landscape. *Journal of Wildlife Management* 65: 92–99.
- Mech, D. 1983. *Handbook of Animal Radio Tracking*. University of Minnesota Press, Minneapolis, Minnesota.
- Millspaugh, J. J., and J. M. Marzluff (eds.). 2001. *Radio Tracking and Animal Populations*. Academic Press, San Diego.
- Millspaugh, J. J., R. M. Nielson, L. McDonald, J. M. Marzluff, R. A. Gitzel, C. D. Rittenhouse, M. W. Hubbard, and S. L. Sheriff. 2006. Analysis of resource selection using utilization distributions. *Journal of Wildlife Management* 70: 384–395.
- Moorcroft, P. R., M. A. Lewis, and R. L. Crabtree. 1999. Home range analysis using a mechanistic home range model. *Ecology* 80: 1656–1665.
- Morrison, J. L., and Stephen R. Humphrey. 2001. Conservation value of private lands for crested caracaras in Florida. *Conservation Biology* 15: 675–684.
- Murray, D. L., and M. R. Fuller. 2000. Effects of marking on the life history patterns of vertebrates. Pp. 15–64. In: *Research Techniques in Ethology and Animal Ecology* (L. Boitani and T. Fuller, eds.). Columbia University Press, New York.
- Nams, V. O. 1989. Effects of radiotelemetry error on sample size and bias when testing for habitat selection. *Canadian Journal of Zoology* 67: 1631–1636.
- Neu, C. W., C. R. Byers, and J. M. Peek. 1974. A technique for analysis of utilization-availability data. *Journal of Wildlife Management* 38: 541–545.
- Neubaum, D. J., M. A. Neubaum, L. E. Ellison, and T. J. O'Shea. 2005. Survival and condition of big brown bats (*Eptesicus fuscus*) after radiotagging. *Journal of Mammalogy* 86: 95–98.
- North, M. P., and J. H. Reynolds. 1996. Microhabitat analysis using radiotelemetry locations and polytomous logistic regression. *Journal of Wildlife Management* 60: 639–653.
- O'Donnell, C. F. J. 2001. Home range and use of space by *Chalinolobus tuberculatus*, a temperate rainforest bat from New Zealand. *Journal of Zoology (London)* 253: 253–264.
- . 2006. Personal communication. Southern Regional Science Centre, Department of Conservation, Christchurch, New Zealand.
- Otis, D. L., and G. C. White. 1999. Autocorrelation of location estimates and the analysis of radiotracking data. *Journal of Wildlife Management* 63: 1039–1044.
- Pace, R. M. 2000. Radiotracking via triangulation: a simple moving windows estimator for describing movement paths. Pp. 517–523. In: *Biotelemetry 15: Proceedings of the Fifteenth International Symposium on Biotelemetry* (J. H. Eiler, D. J. Alcorn, and M. R. Neuman, eds.). Juneau, Alaska. International Society on Biotelemetry. Wageningen, the Netherlands.
- . 2001. Estimating and visualizing movement paths from radio-tracking data. Pp. 126–164. In: *Radio Tracking and Animal Populations* (J. J. Millspaugh and J. M. Marzluff, eds.). Academic Press, San Diego.
- Pendleton, G. W., K. Titus, E. Degayner, G. J. Flatten, and R. E. Lowell. 1998. Compositional analysis and GIS for study of

- habitat selection by goshawks in southeast Alaska. *Journal of Agricultural, Biological, and Environmental Statistics* 3: 280–295.
- Pennycuik, C. J., M. R. Fuller, and L. McAllister. 1989. Climbing performance of Harris's hawks (*Parabuteo unicinctus*) with added load: implications for muscle mechanics and for radiotracking. *Journal of Experimental Biology* 142: 17–29.
- Racey, P. A. 1985. Feeding ecology of *Pipistrellus pipistrellus* during pregnancy and lactation. *Journal of Animal Ecology* 54: 205–215.
- Ratti, J. T., and E. O. Garton. 1994. Research and experimental design. Pp. 1–23. In: *Research and Management Techniques for Wildlife and Habitats* (T. A. Bookhout, ed.). The Wildlife Society, Bethesda, Maryland.
- Rettie, W. J., and P. D. McLoughlin. 1999. Overcoming radiotelemetry bias in habitat-selection studies. *Canadian Journal of Zoology* (London) 77: 1175–1184.
- Rettie, W. J., and F. Messier. 2000. Hierarchical habitat selection by woodland caribou: its relationship to limiting factors. *Ecogeography* 23: 466–478.
- Rydell, J. 1989. Feeding activity of the northern bat *Eptesicus nilssonii* during pregnancy and lactation. *Oecologia* 80: 562–565.
- Samuel, M. D., and K. P. Kenow. 1992. Evaluating habitat selection with radio-telemetry triangulation error. *Journal of Wildlife Management* 56: 725–734.
- Samuel, M. D., and M. R. Fuller. 1996. Wildlife radio telemetry. Pp. 370–418. In: *Research and Management Techniques for Wildlife Habitats*, 5th ed. (T. A. Bookhout, ed.). The Wildlife Society, Bethesda, Maryland.
- Sartwell, J. 2003. The Telemetry Computing Project. Missouri Department of Conservation, Federal Aid in Wildlife Restoration Project. W-13-R, Final Report.
- Schoener, T. W. 1981. An empirically based estimate of home range. *Theoretical Population Biology* 20: 281–325.
- Seaman, D. E., and R. A. Powell. 1991. Kernel home range estimation program. Version 4.26. U. S. Geological Survey, Biological Resources Division, Port Angeles, Washington.
- Seaman, D. E., J. J. Millspaugh, B. J. Kenohan, G. C. Brundige, and K. J. Raedeke. 1999. Effects of sample size on kernel home range estimates. *Journal Wildlife Management* 63: 739–747.
- Shiel, C. B., R. E. Shiel, and J. S. Fairley. 1999. Seasonal changes in the foraging behaviour of Leisler's bats (*Nyctalus leisleri*) in Ireland as revealed by radio-telemetry. *Journal of Zoology* (London) 249: 347–358.
- Silverman, B. 1986. *Density Estimation for Statistics and Data Analysis*. Chapman & Hall, London.
- Smith, R. M., and B. Trevor-Deutsch. 1980. A practical, remotely controlled, portable radio telemetry receiving apparatus. Pages 269–273. In: *A Handbook on Biotelemetry and Radio Tracking* (C. J. Amlaner and D. W. Macdonald, eds.). Pergamon Press, Oxford.
- Smith, P. G., and P. A. Racey. 2005. The itinerant natterer: physical and thermal characteristics of summer roosts of *Myotis nattereri* (Mammalia: Chiroptera). *Journal of Zoology* (London) 266: 171–180.
- Spencer, H. J., and T. H. Fleming. 1991. Roosting and foraging behavior of the Queensland tube-nosed bat, *Nyctimene robinsoni* (Pteropodidae)—Preliminary Radio-Tracking Observations. *Australian Wildlife Research* 16: 413–420.
- Thomas, D. L., and E. J. Taylor. 1990. Study designs and tests for comparing resource use and availability. *Journal of Wildlife Management* 54: 322–330.
- Thomasma, L. E., T. D. Drummer, and R. O. Peterson. 1991. Testing the habitat suitability index model for the fisher. *Wildlife Society Bulletin* 19: 291–297.
- Turchin, P. 1991. Translating foraging movements in heterogeneous environments into the spatial distribution of foragers. *Ecology* 72: 1253–1266.
- . 1996. Fractal analysis of animal movement: a critique. *Ecology* 77: 2086–2090.
- . 1998. *Quantitative Analysis of Animal Movement: Measuring and Modeling Population Redistribution in Animals and Plants*. Sinauer Associates, Inc., Sunderland, Massachusetts.
- White, G. C., and R. A. Garrott. 1986. Effects of biotelemetry triangulation error on detecting habitat selection. *Journal of Wildlife Management* 50: 509–513.
- . 1990. *Analysis of Wildlife Radio Tracking Data*. Academic Press, San Diego.
- Whitehouse, S., and D. Steven. 1977. A technique for aerial radio tracking. *Journal of Wildlife Management* 41: 771–775.
- Wilkinson, G. S., and J. W. Bradbury. 1988. Radiotelemetry: techniques and analysis. Pp. 105–124. In: *Ecological and Behavioral Methods for the Study of Bats* (T. H. Kunz, ed.). Smithsonian Institution Press, Washington, DC.
- Willis, C. K. R., and R. M. Brigham. 2002. Roost switching, roost sharing and social cohesion in forest-dwelling big brown bats. *Bat Research News* 43: 192–193.
- Winterstein, S. R., H. Campa, III, K. F. Millenbah, and T. G. Coon. 2001. Infusing quantification into a fisheries and wildlife undergraduate curriculum: the Michigan State University model. *Wildlife Society Bulletin* 29: 1031–1037.
- Withey, J. C., T. D. Bloxton, and J. M. Marzluff. 2001. Effects of tagging and location error in wildlife telemetry studies. Pp. 43–75. In: *Radio Tracking and Animal Populations* (J. J. Millspaugh and J. M. Marzluff, eds.). Academic Press, San Diego.
- Woeck, R. K., J. J. Millspaugh, and T. W. Mong. 2002. Construction and evaluation of a semi-portable radiotelemetry tower system at Prairie Fork Conservation Area, Missouri. *Transactions of the Missouri Academy of Science* 36: 55–59.
- Worton, B. J. 1989. Kernel methods for estimating the utilization distribution in home-range studies. *Canadian Journal of Zoology* 70: 164–168.
- . 1995. Using Monte Carlo simulation to evaluate kernel-based home range estimators. *Journal of Wildlife Management* 59: 794–800.