Chapter 15
A NASBR History of Radiotelemetry: How Technology Has Contributed to Advances in Bat Biology

Jeff Clerc, R. Mark Brigham, Justin G. Boyles, and Liam P. McGuire

Abstract The first radiotelemetry study of bats was published in 1967, nearly coinciding with the first meeting in 1970 of bat biologists that evolved into the North American Society for Bat Research. Thus, NASBR provides a useful lens to assess the maturation of how this technology has been used in bat research. Researchers may view this developmental process as a purely technological one, as transmitters and receivers have improved dramatically over the last 50 years. However, there has also been growth in the scientific use of radiotracking to do bat research. The earliest studies were question driven and made innovative use of radiotelemetry to answer questions of biological theory previously beyond reach. We suggest that through the 1980s and 1990s there was a technology-driven period, with ever-improving transmitters increasing the number of species within the realm of study. However, researchers also continued to find new types of questions that could be addressed with standard equipment. Finally (and coinciding with the previous period), there has been a shift towards using biotelemetry to address completely different types of questions (e.g., physiological and biophysical). Radiotelemetry has clearly been a boon to bat research, which has allowed us to assess aspects of the ecology, physiology, and behavior of bats that would have otherwise

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been inaccessible. We look forward to the next 50 years of technological improvements and novel research using radiotracking methods.

Keywords Bats · Radiotracking · Radiotelemetry · Technology · Ecology · Behavior · Physiology · NASBR

Radiotelemetry (also referred to as radiotracking or biotelemetry) was first used to track animals in the 1960s (Cochran and Lord 1963), well before the first North American Symposium for Bat Research (NASBR). The first radiotransmitters, used to track rabbits (*Sylvilagus floridanus*), striped skunks (*Mephitis mephitis*), and raccoons (*Procyon lotor*), only cost about $8 for parts ($25 in 2019 dollars) but weighed approximately 10 g (Cochran and Lord 1963). These transmitters were too heavy to affix to almost any New World bat. However, the potential of this technique for studying bats was immediately apparent. Given that bats are volant, nocturnal, and live in spaces that are difficult to access, using telemetry to collect data about them seemed like a natural fit. Donald Griffin (1963), the father of echolocation, postulated that radiotelemetry would be essential to uncover many aspects of their biology and transform the field by allowing researchers the ability to gather data on location and, importantly, continuous longitudinal (temporal) data.

The first bat research involving radiotracking was published in 1967 (Williams and Williams 1967). The authors used 7-g radiotransmitters to track homing flights of displaced greater spear-nosed bats (*Phyllostomus hastatus*; 70–100 g). A second publication followed a few years later (Williams and Williams 1970), coinciding with the first Southwestern Symposium on Bat Research (which became NASBR). Within just a few years, further research using radiotelemetry was reported at NASBR. In 1973, Morrison (Morrison and Bradbury 1973) gave the first talk about data collected using radiotracking. Morrison used ~5-g radiotransmitters to assess foraging by 45–50 g frugivorous Jamaican fruit bats (*Artibeus jamaicensis*) in Panama. Based on these data, Morrison described foraging patterns but, more importantly, also tested hypotheses related to broader ecological theory on foraging, including the influence of habitat, energy budgets, and lunar phobia (Morrison 1978a, b, c, d).

15.1 A Framework for Considering the History of Radiotelemetry and Bats

Since the early studies, radiotelemetry has become a methodological staple in the study of bats. Bat biologists have sought new opportunities as the technology developed, expanding the types of phenomena that have been described and explained. Throughout the history of its application to bats, radiotelemetry has been applied to answer questions about nearly all aspects of chiropteran life history.

Our goal is to characterize the use of radiotelemetry for bat research and determine how technological maturation has taken place. We discuss the history in the context of a technology life cycle, which we envision as occurring in three phases: initial application, proliferation, and categorical application shifts (henceforth application shift).

The first phase of our suggested cycle involves the application of a new technology in a research field; it occurred for bats with the initial radiotelemetry investigations in the late 1960s and early 1970s. For bat researchers, radiotelemetry provided a novel technique that allowed them to overcome the challenges of tracking a moving animal at night. In the initial application phase, we expected to find only a few projects, largely hypothesis-driven, as researchers used the method to address questions that were previously challenging.

After the initial technical hurdles have been surmounted and as the research community becomes aware of the potential of a technique, its use commonly proliferates. In the case of radiotelemetry, refinements include decreased cost, decreased transmitter mass, increased battery life, and improved digitization, making radiotelemetry suitable to collect larger sample sizes for ever-smaller animals. During the proliferation phase, we expected the use of the technique to increase, resulting in a mix of novel, hypothesis-driven projects, as well as descriptive studies that primarily fill gaps in knowledge of natural history.

Following proliferation and refinement of the technique, the third phase of our proposed framework is characterized by innovation and application shifts (i.e., changes in the technology that alter the focus and nature of questions being asked). In this phase, technological advances go beyond simply refining the technique to producing new research opportunities. In the case of radiotelemetry, the ability to use radiotransmitters for remote measurement of skin temperature for metabolic studies is a notable example. This approach still makes use of radiotelemetry, but rather than variations on projects focused just on the animal's location, this application shift enables novel questions to be addressed. As innovations are introduced, each will then follow the patterns described in phase one (application of novel tools) and phase two (proliferation and refinement). Importantly, overlap likely occurs between phases two and three because technological innovations arise (phase three) as techniques continue to proliferate and be refined (phase two).

15.2 Data Collection

The first published studies on bats using radiotelemetry roughly coincided with the first NASBR, and thus NASBR provides a useful lens through which to consider this history. With the three-phase technological framework in mind, we used presentations at NASBR to generate a dataset on the manner in which radiotelemetry has been used and how it has changed. While compiling these data, we noted key developments and other milestones to provide a chronological perspective. In their research on Jamaican fruit bats, Morrison and Bradbury (1973) used radiotelemetry data to address questions and ecological theory rather than just describing patterns. In our analysis, we asked how the relative frequency of such hypothesis testing and descriptive presentations changed over time, as we predicted would occur during the proliferation and refinement phase. Furthermore, we identified the species and types of questions that have been the focus of radiotelemetry papers presented at NASBR.

Our review spanned 48 years of NASBR (1970–2017; except 1978, 1980 and 1982, for which we could not access abstracts). Records from 1970–1975 included only titles and not abstracts, but we are confident that we identified nearly all relevant presentations during this period. For abstracts that explicitly reported use of radiotelemetry, we identified the target species and dependent variables noted in the abstract (e.g., roost, foraging, habitat use, thermoregulation), and determined whether independent explanatory variables (e.g., landscape features, sex, temperature, weather) were also mentioned.

15.3 A General (Semi-Subjective) Timeline of Radiotelemetry at NASBR

In the years following Morrison's presentation, there were few presentations based on radiotelemetry data at NASBR (Fig. 15.1a, b). However, consistent with the first phase of a technology life cycle, these early presentations tended to test broad

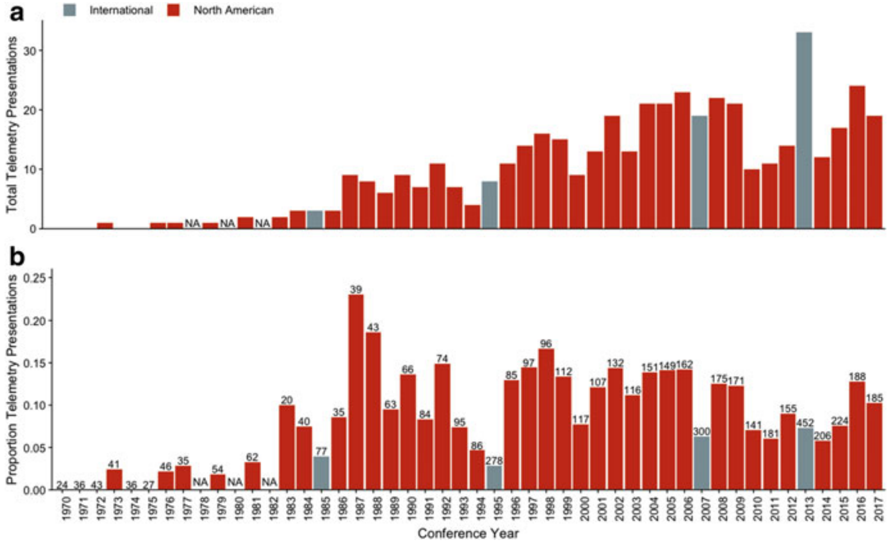

Fig. 15.1 (**a**) Number of presentations at NASBR that involved radiotelemetry. (**b**) Proportion of presentations in each year that involved radiotelemetry. Total number of presentations each year is included atop each bar. International refers to years when NASBR held joint meetings with the International Bat Research Conference. Abstracts from 1978, 1980, and 1982 were not available

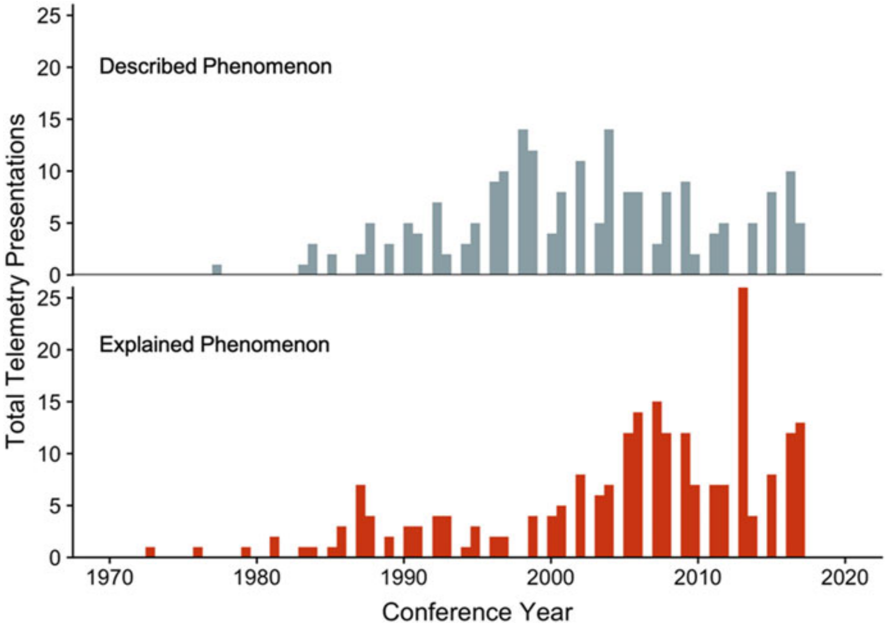

Fig. 15.2 Number of NASBR presentations through time, representing hypothesis-driven presentations (explained phenomenon) and natural history presentations (described phenomenon)

ecological hypotheses and develop ecological theory (Fig. 15.2). A good example was Heithaus and Fleming (1976) who used 2-g radiotransmitters to follow foraging Seba's short-tailed bats (*Carollia perspicillata*; 17–22 g) in Costa Rica, testing theories of refuging and foraging (Fleming et al. 1977; Heithaus and Fleming 1978). Consistent with the idea of a technique being adopted slowly, it was 13 years after the first radiotelemetry presentation at NASBR before a meeting featured more than three presentations about data collected using radiotelemetry. Some intervening years included no presentations, indicating that use of the procedure was limited (Fig. 15.1).

Beginning in the 1980s, the number of presentations that used radiotelemetry rapidly expanded. It became a standard method for tracking bats to roosting sites and foraging areas, and for describing habitat use. Frequent use, consistent with the expectations of the second phase, has continued to the present, with 5–15% of recent presentations at NASBR relying at least in part on telemetry.

Along with increased use came standardization in protocols and guidelines for how radiotelemetry should be employed. A chapter on telemetry (Wilkinson and Bradbury 1988) was included in the book "Ecological and Behavioral Methods for the Study of Bats" which was updated with a chapter in the second edition (Amelon et al. 2009). Other publications provided specific guidance and recommendations. For example, Aldridge and Brigham (1988) suggested a "5% rule" for the maximum ratio of transmitter mass to body mass (compared with 10% or more of body mass in

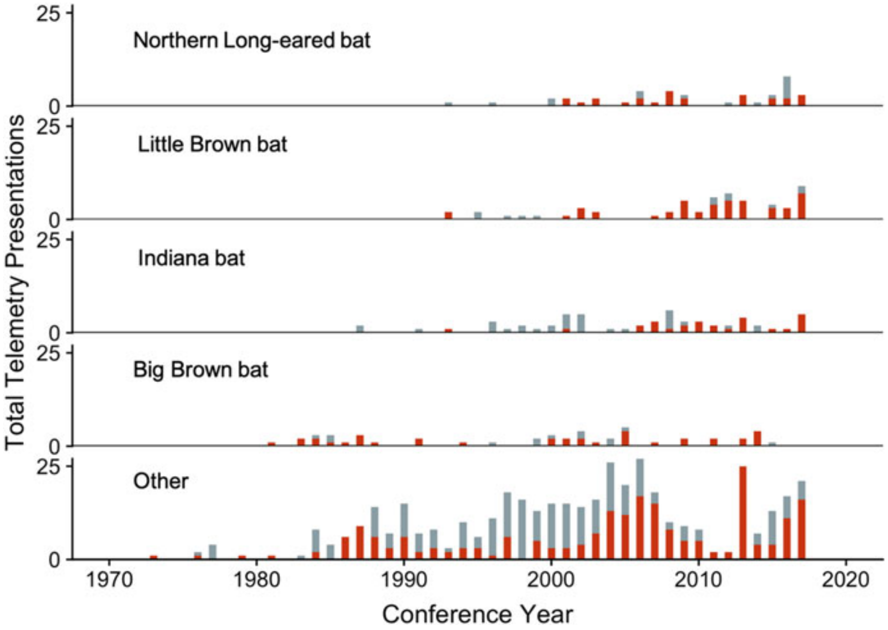

Fig. 15.3 Presentations at NASBR related to species that have more than 30 occurrences in the dataset. Red bars represent hypothesis-driven presentations (explained phenomenon) and grey bars represent natural history presentations (described phenomenon)

early studies; Morrison 1978a, Heithaus and Fleming 1978), and O'Mara et al. (2014) reviewed methods for attaching transmitters to bats.

Again, consistent with the expectations of proliferation in phase 2, the 1980s and 1990s were also a period of technological refinement that led to smaller (~1-g; Geggie and Fenton 1985) and less expensive transmitters. During this phase, the number of presentations using a hypothesis-testing approach was consistently small, but the number of descriptive or natural history presentations grew rapidly (Fig. 15.2). A large part of this latter trend was attributable to the greater presence at NASBR of personnel from government and conservation agencies and the realization that bats were also "wildlife," which provided evidence that technology patterns were influenced by "societal" trends.

Most early projects focused on larger species with body mass of at least 20 g, such as the greater spear-nosed bat (Williams and Williams 1967, 1970), Jamaican fruit bat (Morrison and Bradbury 1973), Seba's short-tailed bat (Heithaus and Fleming 1976), and big brown bats *Eptesicus fuscus* (Geggie and Fenton 1985). By the mid-1990s, studies of small species of *Myotis* spp. became more common (Fig. 15.3). This was in large part agency-driven, as telemetry was increasingly used to study endangered species, especially Indiana bats (*Myotis sodalis*). Through the history of the meetings, 112 different species of bats have been the topic of presentations at NASBR, which does not include one of the co-authors of this

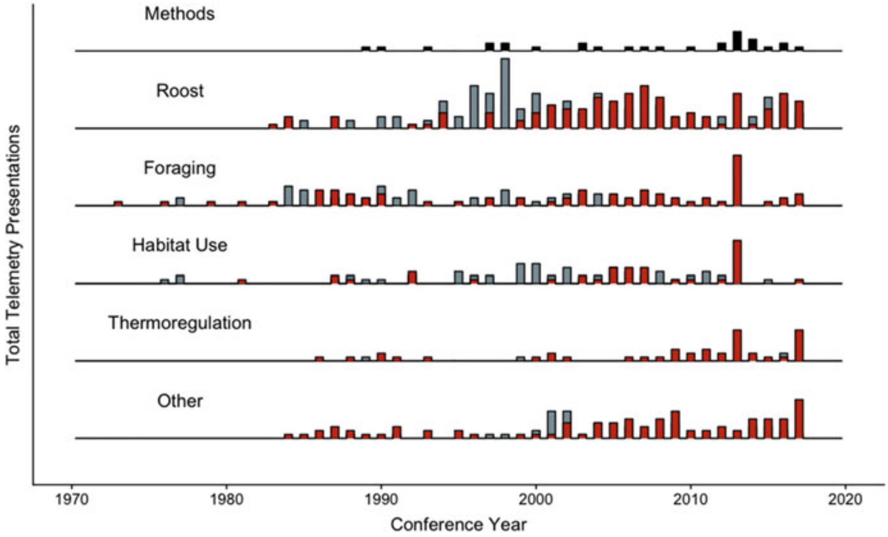

Fig. 15.4 Subject of radiotelemetry presentations by year at NASBR. Methodological presentations first appeared in 1989 and have since been a regular feature. Our main analysis focused on presentations of biological questions and observations with dependent variables including roost, foraging, habitat use, thermoregulation, and other biologically relevant dependent variables. Grey bars represent natural history presentations and red bars represent presentations involving hypothesis testing

chapter repeatedly reporting data on "feathered bats" (i.e., nightjars). From this long list, several species were a common focus, with four species (by rank order: Indiana bat; little brown bat, *Myotis lucifugus*; big brown bat; and northern long-eared bat, *Myotis septentrionalis*) each featured in more than 30 presentations (Fig. 15.3). Members of a second tier of species were each the focus of more than 15 presentations (by rank order: silver-haired bat, *Lasionycteris noctivagans*; hoary bat, *Lasiurus cinereus*; Rafinesque's big-eared bat, *Corynorhinus rafinesquii*; and eastern red bat, *Lasiurus borealis*). Most species (n = 75) were the focus of only one or two presentations.

Through the period of proliferation and technological refinement, additional species to the original large bats were studied, but the types of questions addressed remained limited. Most presentations during phase one focused on foraging, followed soon after by research on roosting sites, and then general habitat use (Fig. 15.4). During the proliferation period, presentations titles following the format "roosting and foraging areas of species X, in location Y" were common. Studies evaluating hypotheses about habitat selection remained infrequent, likely due to the logistic challenges of actively tracking small animals moving over large distances. Conversely, because tracking an individual to a daytime roost is relatively straightforward, research on roost selection became particularly prevalent in the mid-1990s. Much of the research during this time was driven not only by technological refinement but also by policy and funding. For example, regulatory agencies had a strong

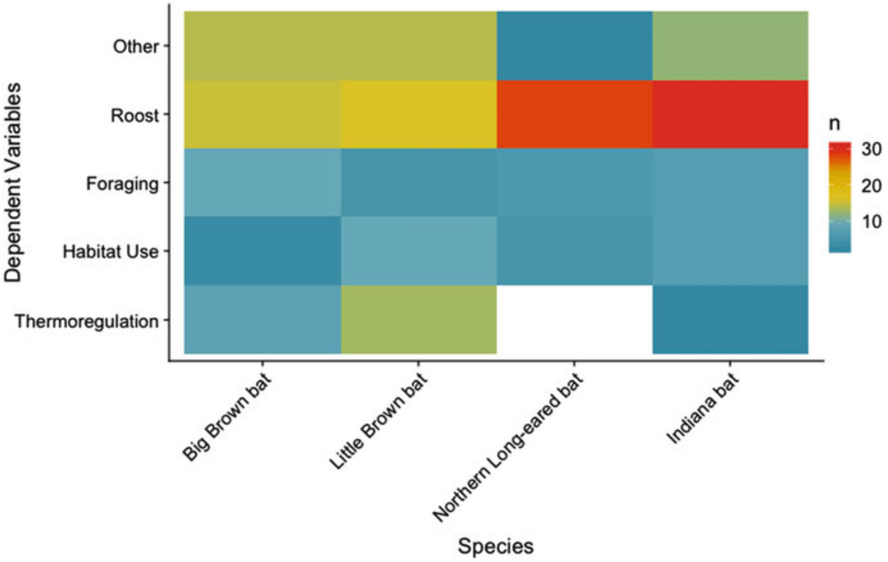

Fig. 15.5 Heat map representing the number of times a topic and species occur together in the dataset, focusing on species that are referenced over 30 times in the dataset

interest in the roosting and foraging habitat of the Indiana bat, an endangered species in the United States, providing both incentive and financial resources for such investigations. Consequently, beginning in the 1990s, reports on roosting ecology of Indiana bats became a dominant feature of radiotelemetry presentations at NASBR (Fig. 15.5). This phenomenon skews the types of hypothesis-testing presentations and these investigations have been overwhelmingly focused on roost selection in relation to landscape features (Fig. 15.6). This same trend is apparent in a recent spike in presentations about northern long-eared bats (Fig. 15.5), listed as endangered in Canada in 2013 and threatened in the United States in 2015, due to white-nose syndrome.

Research on migration has also benefited from refinements in radiotelemetry technology, as evidenced by the second tier of commonly studied species. Of the four species in that tier, three are long-distance migrants: silver-haired, hoary and eastern red bat. However, tracking migratory movements is challenging. Early migration studies relied on banding and mark-recapture efforts, which provide limited, albeit valuable, data (Ellison 2008). Some studies have followed migrating bats with road vehicles and aircraft (e.g., Britzke et al. 2006; Roby et al. 2019), but maintaining consistent contact with a bat over multiple nights and potentially hundreds of kilometers is difficult and greatly limits sample size. This affects the inferential scope of the results. Recently developed, digitally coded radiotransmitters broadcast unique identifiers on a common frequency, enabling more individuals to be tracked and allowing extended migratory movements to be determined. The

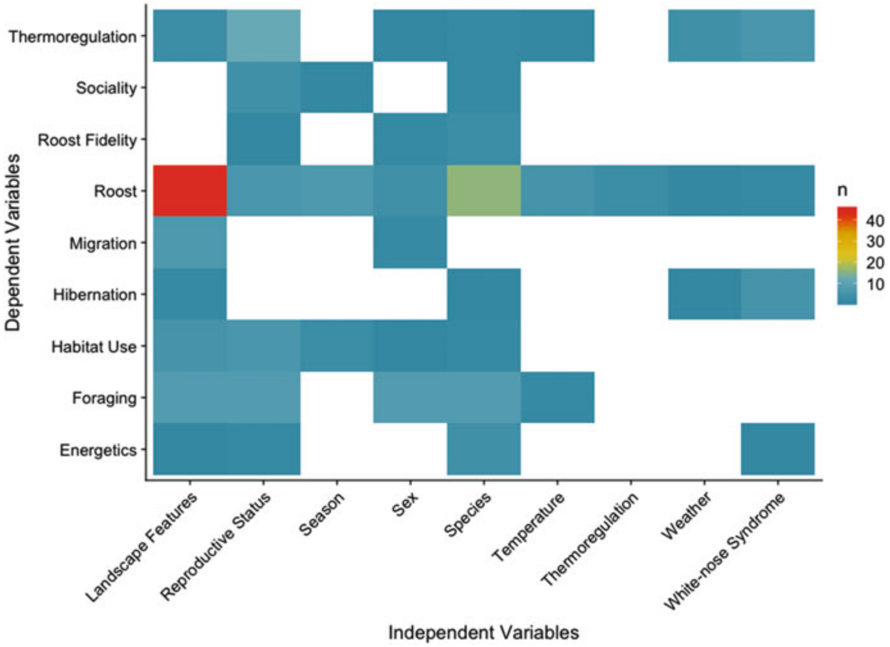

Fig. 15.6 Heat map representing the number of times a dependent and independent variable occur together in the dataset, showing combinations that have been investigated in greater than five presentations at NASBR

Motus Wildlife Tracking System (motus.org), for example, consists of stationary receivers deployed across the landscape, which detect any transmitters that come within range (e.g., McGuire et al. 2009; Jonasson and Guglielmo 2014; McGuire 2018). Although not suitable for all species, such systems have the potential to enhance our understanding of long-distance migratory movements.

Through the period of proliferation and refinement, there remained a number of hypothesis-testing presentations (Fig. 15.2). Nevertheless, the dominance of presentations on roost selection in relation to landscape features (Fig. 15.6), particularly for one or two species (Fig. 15.5), skews this interpretation. We feel it is more informative to consider cases of truly novel hypotheses and investigations that arise from new uses of radiotelemetry. For example, locations provided by radiotelemetry have been used to investigate fission-fusion dynamics and questions of sociality (e.g., Willis and Brigham 2002; Johnson et al. 2010). These projects relied on the basic technology and information gathered about the locations of individuals but addressed new questions. Similarly, radiotelemetry has been an important tool for investigating aeroecology. For instance, McCracken et al. (2016) used aircraft to track Brazilian free-tailed bats (*Tadarida brasiliensis*) over long-distances, to answer questions about flight dynamics relative to regional wind patterns.

The third phase of our conceptual framework predicts categorical shifts in the application of radiotelemetry. These are changes that are not simply the result of proliferation and refinement of technology, but instead technological innovation and novel approaches in how the technique is used. In the case of bat research, we consider this phase to be defined primarily by use of radiotransmitters that provide more than just location data. Caceres (1965) was the first to speak to biomedical telemetry. Temperature-sensitive radiotransmitters were first introduced for ecological research in 1972 (Osgood and Weigl 1972) and the first publication involving bats was Weigold (1973). However, it was not until 1988 that this application shift appeared in a presentation at NASBR, when Hickey (1988) discussed the use of torpor by hoary bats that carried temperature-sensitive transmitters. Thermoregulation has always been a well-studied topic in bats, first in the context of torpor and hibernation (Hock 1951) and later in the context of migration (e.g., McGuire et al. 2012), and therefore, it is perhaps not surprising that thermoregulation has become the second most common subject of presentations featuring telemetry data (Figs. 15.4 and 15.6).

There are several other examples of application shifts in use of radiotelemetry, although few have been widely adopted yet. Similar to the development of temperature-sensitive transmitters is heart-rate telemetry, which has been used to measure stress responses (Allen et al. 2008) and energetics (O'Mara et al. 2015). Only four presentations at NASBR have reported using this technology. Other new telemetry-based technologies have enabled researchers to track the altitude at which bats fly (O'Mara et al. 2019) or detect wing-beat frequency to identify alternating periods of powered flight and gliding (Kunz et al. 2014; McCracken et al. 2016). Despite the limited number of studies, these application shifts and technological advancements illustrate the exciting potential that further development and innovation can bring, allowing a diverse range of new questions to be addressed.

15.4 Looking Back and Looking Forward

The timeline of NASBR coincides with the timeline of radiotelemetry as a technique to study bats. Through the past 50 years, the data are consistent with a progression through all three phases of a technology life cycle. Early studies were few and focused on answering questions related to biological theory. In a short time, the technique was refined and proliferated throughout the research community, a process that has continued as application shifts provided methods to answer more diverse biological questions.

Technology has long been a key to new research avenues and is often necessary to address old questions in new ways. However, despite the ubiquity of radiotelemetry, the cost of radiotransmitters and associated equipment has generally limited sample sizes. The price of transmitters has declined over time, but the market for wildlife research is relatively small compared to other commercial areas. The small sample size in many telemetry studies presents a challenge for testing hypotheses, and sometimes contributes to research that is primarily descriptive in nature. Such reports can be informative, but increasing the sample, scale, and scope of investigations can lead to major advances in understanding. In the future, we hope that researchers will form collaborative networks that will enable pooling of resources to allow questions to be addressed at broader scales (e.g., Taylor et al. 2017).

The first 50 years of NASBR have served witness to amazing uses of radiotelemetry. This method has illuminated many aspects of the biology of bats that were otherwise cryptic. As we move into the next 50 years of the society, we predict it will be equally exciting to watch new technologies emerge and reveal aspects of the lives of bats which are currently unknown. We expect to see innovations in both transmitter capability (e.g., further miniaturization, increased availability of sensors, and more efficient digitization) and receiver technology (e.g., increased sensitivity, availability, and the ability to interface with satellites [Wikelski et al. 2007]), as well as increasing use of related systems like GPS (e.g., Weller et al. 2016). Further refinement of existing technology will lead to incremental advances, but innovative new approaches, such as powering transmitters with energy harvested from the movement of the animals (Shafer et al. 2015), may lead to major advances. With refinement of existing sensor technologies and better electronics, it will be possible to combine multiple sensors into a single transmitter (Gumus et al. 2015), providing opportunities to integrate multiple datasets from individual animals. We also hope to see transmitters used in completely new ways. Over the next 50 years of NASBR, telemetry may be used to address biological questions holistically from molecular to ecosystem scales (i.e., integrating information gathered from radiotelemetry with broader levels of biological organization). Likewise, manipulating bats by delivering drugs using telemetry for either experimental design or conservation reasons greatly increases the possible uses.

With ever-advancing technology, we encourage bat biologists to not fall into the trap of using the new technology and then searching for a question, but instead to seek answers to questions that require advances in technology. This latter approach is superior scientifically and will help drive technological advances. The biggest leaps in the field will come from solid research practices and hypothesis-driven research allowing for strong inferences, in essence, phase one of the technology cycle. Biologists have many tools with which to gather data to address diverse questions. Radiotelemetry has certainly become a regular tool used by bat biologists, but as highlighted by our analysis of NASBR presentations, radiotelemetry can be a versatile and ever-developing tool. From the first studies with large transmitters that provided only location data on a limited number of large species, we have seen a rapid diversification in the range of species studied and the types of questions that are investigated. Early studies focused on the relatively simple question of “Where is the animal?”, but modern radiotelemetry enables us to address questions about locations, movements, sociality, energetics, and behavior to name just a few. Although the novelty of the technique has long since worn off, each year at NASBR we look forward to the latest and greatest research using radiotelemetry.

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