Summary and Analysis of the U.S. Government Bat Banding Program

By Laura E. Ellison

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Upper left: Little brown bat (*Myotis lucifugus*) banded with USFWS band. Photograph by Merlin D. Tuttle, Bat Conservation International.

Center left: Representative USFWS bands in 3 sizes (No. 0, 1, 2) issued by the Bat Banding Program. Photograph montage by Alfred L. Gardner.

Lower left: Gray bat (*Myotis grisescens*) banded with USFWS band. Photograph by Merlin D. Tuttle, Bat Conservation International.

Right: Little brown bat (*Myotis lucifugus*) banded with USFWS band. Photograph by Merlin D. Tuttle, Bat Conservation International.

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Executive Summary

This report is a summary of the Bat Banding Program (BBP) administered, coordinated, and maintained by the U.S. Bureau of Biological Survey in the Department of Agriculture and its successor, the U.S. Fish and Wildlife Service in the Department of the Interior from 1932 to 1972. Bands were issued and copies of the permanent records were maintained at the Bird and Mammal Laboratories, U.S. National Museum, Washington, D.C., during the active parts of the program (1932–72). Following various agency transfers within the Department of the Interior, the files and documentation for this program are currently maintained in the same location, but under the USGS, Patuxent Wildlife Research Center, Biological Survey Unit at the Smithsonian Institution, National Museum of Natural History, Washington, D.C.

More than 2 million bat bands were issued by the BBP from 1932 to 1972, of which approximately 1.5 million were applied to 36 species of bats by scientists, their students, and colleagues in many locations in North America including the United States, Canada, Mexico, and Central America. Banding activities were also conducted in Argentina, Iran, and Puerto Rico. Many interesting facts about basic bat biology were discovered by the application of these bands including homing behavior, return rates, distances bats are capable of traveling, longevity, seasonal migrations, hibernation ecology, mortality and survival rates, and reproductive behavior. Throughout the program, bat banders noticed numerous and worrisome deleterious effects on bat health and survival. This led to experimentation with different types of bands applied to different parts of bats' bodies for several decades. However, the problem of injuries to bats was deemed so serious that a moratorium on bat banding was suggested in 1972 and was later ratified by members of the American Society of Mammalogists at its annual meeting in June 1973. One of the main points of the memorandum written to justify the moratorium was to conduct a "detailed evaluation of the files of the bat-banding program." The overall purpose of this evaluation was to determine the value and relevance of the biological data that were accumulated in the files, and to study the feasibility of automated techniques for the storage and retrieval of data if the program were to continue. However, the program did not continue except to issue a few bands to researchers conducting ongoing, long-term studies and to file and maintain information from recoveries to the current day. This report is an effort to satisfy the need for a comprehensive review and critical evaluation of the BBP and its associated files.

I have four major goals for this report: (1) To provide a detailed history and summary of the BBP and its corresponding files; (2) to provide an overview of the utility of the existing BBP files to answer specific questions about bat population biology using mark-recapture techniques; (3) to provide a case study in data management and survival analysis of a long-term banding effort from the program; and (4) to make recommendations about the future uses of the files and suggestions for maintaining and organizing any large-scale marking program. My first goal involves compiling

a history of the BBP, describing the logistics and methods for maintaining the files, providing a comprehensive survey and analysis of the literature specific to the program and discussing known problems with the banding files illustrated with specific case studies. My second goal includes a discussion of the utility of the BBP files for answering questions about bat population biology. This includes an overview of mark-recapture techniques and what parameters can be estimated by banding or otherwise individually marking bats. My third goal is to provide a case study in managing data and applying current mark-recapture theory to estimate survival using the information from a series of bat bands issued to Clyde M. Senger during the BBP. Senger banded bats in the State of Washington from fall of 1964 until the winter of 1975 with resightings noted until as late as winter 1980. He and his associates banded eight different bat species, but the majority of bands were applied to Townsend's big-eared bat (*Corynorhinus townsendii*), a species of special concern for many States within its geographic range, including Washington (*http://wdfw.wa.gov/wlm/diversty/soc/soc.htm*). This species is considered a Federal Species of Concern (formerly Category II [C2]) by the U.S. Fish and Wildlife Service (U.S. Fish and Wildlife Service, 1994; Pierson and others, 1999). I also discuss the results from this retrospective analysis and the value of the population estimates derived in relation to conducting future mark-recapture analyses of the BBP files, which would involve a considerable effort to computerize the files. My final goal is to provide specific recommendations for the future of the BBP files, future bat-marking efforts, and establishing a Web-based clearinghouse for studies involving marked bats.

The BBP dealt with numerous problems during its entire tenure. The three main problems were issues with the bands, disturbance to bat populations from research and banding activities, and problems with the BBP files and recoveries. Bands not only caused direct injuries to bats but were frequently chewed by the bats so that the numbers would become illegible. The quality of the bands varied throughout the program; some bands were made from such a soft aluminum alloy that they would not last beyond a single season after banding. There was no consistency in the type of band used on bats due to constant experimentation with different types of bands in an attempt to find a less injurious, longer-lasting means of individually marking bats. Disturbance by banding at bat roosts was implicated in bat population declines in 22 North American species because banding activities commonly would occur during critical periods such as hibernation or periods of recruitment. Finally, the BBP files were incomplete and not well organized, with many instances of reporting errors, which compromised information based on recoveries and recaptures. Overall recoveries and recaptures of banded bats were low. The retrospective analysis of a select dataset in the BBP files provided relatively precise estimates of survival for wintering Townsend's big-eared bats; however, this dataset was unique due to its being well maintained and complete and because recapture rates were high over the course of banding. It is doubtful that any other unpublished datasets of the same quality exist buried in the BBP files for further analyses.

Based on the findings from this report, I make the following three recommendations: (1) The BBP files should not be computerized in their entirety because the resulting analyses would provide no additional information of value to our current knowledge of population biology of bats; (2) marking bats with standard metal or split-ring forearm bands should not be considered for mark-recapture studies unless the information sought and the potential for obtaining unbiased estimates from that information vastly outweighs the potential negative effects to the bats; and (3) a Web-based clearinghouse can be developed to serve as a centralized resource on bat-marking methods, mark-recapture techniques, and for the exchange of information on marked bats.

Format of Report

This report is divided into four parts. Part 1 provides a detailed summary of the BBP including a history and overview, knowledge gained from bat banding, and known problems with case studies. In Part 2, I discuss mark-recapture techniques and the utility of the existing BBP files to answer questions about the population biology of bats. Part 3 provides a case study in the data management and analysis of banding data on Townsend's big-eared bats with a discussion on the value of post hoc analyses using the BBP files. Part 4 not only summarizes findings from the first three parts, it also provides a list of suggestions for the future of the BBP files and any future standardized bat-marking program. I provide a list of bat banders in Appendix 1, a copy of the policy detailing the moratorium to desist bat banding in Appendix 2, and basic summaries from the literature survey in Appendix 3.

Part 1. History and Overview of the Bat Banding Program

Introduction

More than 2 million bat bands were issued by the Bat Banding Program (BBP) from 1932 to 1972 of which approximately 1.5 million were applied to 36 species of bats by scientists, their students, and colleagues in many locations in North America including the United States, Canada, Mexico, and Central America. Hereinafter, the Bat Banding Program will be referred to as the BBP, bat bands issued by the BBP will be called USFWS bands, and the files for the program will be called the BBP files. For notification purposes when bands were recovered, the majority of the bands produced were stamped with either "F&W SERV" or "FWS"; hence, I made the decision to call them "USFWS bands" for consistency. Many interesting facts about basic bat biology were discovered by the application of USFWS bands, including homing behavior, return rates, distances bats are capable of traveling, longevity, seasonal migrations, hibernation ecology, mortality and survival rates, and reproductive behavior. Throughout the BBP, banders noticed numerous and worrisome deleterious effects on bat health and survival. This led to experimentation for several decades with different types of bands applied to different parts of bats' bodies. However, the problem of injuries to bats was deemed so serious that a moratorium on bat banding was suggested in 1972 and was later ratified by members of the American Society of Mammalogists at an annual meeting in June 1973. One of the main points of the memorandum written to justify the moratorium was to conduct a "detailed evaluation of the files of the bat-banding program." The overall purpose of this proposed evaluation was to determine the value and relevance of the biological data that were accumulated in the files, and to study the feasibility of automated techniques for the storage and retrieval of data if the program were to continue. However, the program did not continue except to issue a few bands to researchers conducting ongoing, long-term studies, and to file and maintain information from recoveries to the current day. A full evaluation of the information in the BBP files was never completed.

The purposes of this part are to provide a history of the BBP, describe the logistics and data-collection methods used to maintain the files of banding information, summarize the knowledge we have gained with the use of bat bands based on findings from a detailed literature review of banding during the program, and finally, discuss the known problems with bat banding and with the overall program illustrated with specific case studies. This overview expands on several other summaries of the BBP published previously (Mohr, 1952; E.L. Davis, 1968; Greenhall and Paradiso, 1968; O'Shea and others, 2004; Peurach, 2004). The last overview of the

BBP in existence is the "History and Current Status of the Bat Banding Office, National Museum of Natural History" published in *Bat Research News* in 2004 (Peurach, 2004).

Sources of Information

I used three main sources of information to create this history and overview of the BBP:

1. I conducted a comprehensive literature review of banding efforts during the period of the BBP. I found literature related to banded bats primarily in peer-reviewed journals, but I also included agency reports, unpublished theses and dissertations, and other "gray" literature. I focused this literature review on studies that used bands supplied by the BBP; hence, files were also maintained by the program about the banders, how many bats they banded, and any recoveries that were reported.

2. I reviewed every issue of *Bat Research News*. This publication began as a newsletter called *Bat Banding News* from 1960 to 1963 before its name change to *Bat Research News*. Many of the early volumes of this publication contained information about bat-banding efforts using USFWS bands, the ongoing experimentation with different types of bands and marking techniques, and incidental reports of band recoveries.

3. I spent a week in August 1996 investigating the BBP files located at the USGS, Patuxent Wildlife Research Center, Biological Survey Unit at the Smithsonian Institution, National Museum of Natural History, Washington, D.C. The BBP files not only include approximately 90 drawers of 3×5-inch index cards with banding information, but also include files of correspondence (memoranda), gray literature, anecdotal information on handwritten pieces of paper, and copies of publications about banding efforts. I reviewed and copied pertinent information including memoranda from these files but could not include copies in this document because of the poor quality of the copies.

History of Bat Banding and the Program

Early Banding

The individual marking of bats in the United States had its earliest beginnings in 1916 with the application of bird bands to the legs of four eastern pipistrelles (*Perimyotis subflavus*) (Allen, 1921; Greenhall and Paradiso, 1968). A few small-scale banding efforts were conducted in the 1920s in California, Pennsylvania, and Florida, but it was not until 1932 that banding became a sustained effort with the work of D.R. Griffin, E.L. Poole, and C.E. Mohr. It was also in 1932 that the use of bird bands was officially sanctioned for use on bats and the U.S. Biological Survey considered the coordination and issuing of bands for bats an official "program" and "clearinghouse." In the middle to late 1930s, the program expanded in number of banders and number of bats banded, but during World War II banding activities ceased. In the 1950s, the number of bands issued increased significantly (Greenhall and Paradiso, 1968). By the end of 1951, Mohr (1952) estimated that 67,403 bats had been banded in North America.

During the first decade of the BBP (1932–39), there was considerable confusion as to the best way of marking bats, and bat researchers experimented with different ways of marking bats and different placement of marks. C.E. Mohr explored staining, stenciling, and tattooing but found that something more permanent was needed to mark bats (1933a; 1934). After hearing about

Allen's work marking bats with aluminum bird bands, he requested a supply of bands from the U.S. Biological Survey (Mohr, 1934). His request was denied by the BBP, citing that Luther Little of Howell and Little (1924) had found the aluminum USFWS bands "unsatisfactory, the numbers having been almost completely worn off the aluminum tags during the years the bats were at large." Independently, Mohr tested the efficacy of banding using 100 bands on his own. He attached bands to the leg by cutting a slit in the interfemoral membrane close to the tibia, slipping one end of the band through and pressing it shut on the opposite side of the leg. He found that recoveries a year later showed no ill effects, but it was necessary to press the membrane to one side to read the band number. He found leg bands were impossible to detect in clusters of hibernating bats, so he experimented with metal tags used on fins of small fishes ("fingerling" tags). To study homing behavior and movements, he attached fingerling tags to the ears of three species: little brown myotis (*Myotis lucifugus*), eastern pipistrelles, and northern long-eared myotis (*Myotis septentrionalis*). Some banders believed that tags attached to the ear of a bat could potentially disrupt behavior or navigation; however, one of Mohr's ear-tagged bats was known to have survived 13 years (BBP file recovery), suggesting that at least for this individual, there was no serious impairment (Hitchcock, 1960). Mohr continued to use a combination of fingerling ear tags and aluminum leg bands in his studies of Pennsylvania bats during this early banding period (Mohr, 1933b, 1934, 1936, 1942a, 1942b). It was not until 1937 that Mohr was able to purchase 2,500 aluminum ear tags (stamped "Notify U.S. Biol. Surv.") and continue his banding under the auspices of the BBP or "clearinghouse" (Mohr, 1939).

Two other early banders were D.R. Griffin and E.L. Poole. In the mid-1930s, D.R. Griffin experimented with two methods of marking a colony of little brown myotis (Griffin, 1934). He tattooed numbers on the wing membranes and banded on the leg with USFWS bird bands (No. 0). He found tattooing to be less useful because it required more time to apply and required close examination of the bat. He found bands were more quickly applied and were more plainly visible. Additionally, only a number could be tattooed on the bat's wing, whereas a band could also bear the return address for notification if the bat was found by someone else. D.R. Griffin continued to band bats on the leg even though a concurrent study in Germany showed that bats could be banded on the forearm (Eisentraut, 1934; Griffin, 1936; 1940a; 1945). E.L. Poole stained bats' wings with haemotoxylin, a yellow-brown natural dye, for a homing study in Pennsylvania in 1931 (Poole, 1932). Several bats were recovered back at their cave of capture, but it was very clear something more permanent was needed to mark the bats. Excellent summaries of these early banding efforts and experimentation with different marking techniques were published by Griffin (1936, 1940a, 1945) and Mohr (1952).

Banding bats on the hind leg was the standard technique for these early banders up until 1939. Trapido and Crowe (1946) began banding on the forearm in 1939, and this became the standard band placement during the remainder of the BBP. However, confusion and controversy still existed among bat banders as to the style and size of bands to use on bats. Up until 1955, most bats were banded with standard aluminum bird bands. The sharp metal edges of bird bands, especially at the corners, would often cut into the wing membranes of bats and cause flesh to grow over the ends of the band (Hitchcock, 1957). Evidence of injuries and death to bats from bands was the impetus for developing a new "lipped" band based on a Dutch design. Some of these lip-end type bands were issued by the BBP beginning in the mid-1950s until the banding moratorium in 1973. However, straight-edged bird bands were also simultaneously issued up until the end of the program (C.M. Senger, oral commun., 2008). There were also four different sizes of bat bands available: 0, 1A, 1, 2. I could not find any evidence in the BBP files of size 1A bands being issued or applied to bats. The "0" was the smallest and No. 2 the largest. Banders debated which size was best for North American bats; some thought small-sized bands should be applied to small-sized bats, and the reverse. The No. 2 band was the most popular and constituted about 90 percent of the bands issued during the entire program, but some banders believed this size of band was too big for some species of bats (Greenhall and Paradiso, 1968). The BBP published a comprehensive "Bat-banding Manual" in 1968 that summarized the early history of bat banding, described techniques for locating bat roosts and capturing bats, described banding techniques and how to record data, and warned about some of the main health issues to be aware of when handling bats (for example, rabies, histoplasmosis; Greenhall and Paradiso, 1968).

Bat Banding News/Bat Research News

Beginning in the early 1960s, the history of bat banding in North America was closely tied to the publication *Bat Research News*. The newsletter was originally called *Bat Banding News* from 1960 to 1963 (edited by W.H. Davis) for the first four volumes (14 issues) (Davis, 1984). The early issues of *Bat Banding News* focused on bat-banding issues, including quite a bit of anecdotal information on band injuries (Davis, 1960a). Other articles addressed tips on equipment, catching bats, handling bats, locating colonies, problems of general interest such as rabies, banding tree bats, the use of nets, a better bat band, the disappearance of Indiana bats (*Myotis sodalis*) in summer, notes on individual banders and their studies, and a frequent listing of names and addresses of active banders (Davis, 1960b). *Bat Banding News* was not a comprehensive resource for bat banding because of its early status as a newsletter. Interesting longevity records and new insights into species biology because of banding activities were therefore not always included because there was the potential for other journals to view subsequent submissions as unoriginal (Davis, 1963).

Bat Banding News became *Bat Research News* in 1964 to address the growing interest in all aspects of bat biology, not just issues related to banding bats (Davis, 1964a). W.H. Davis continued as the editor until 1970. Interesting facts about banding bats continued to be published in the newly named newsletter, however. For example, in the first issue with its new name, there was a notice to active bat banders stating that the number of bands issued for use on bats had increased about 2,000 percent since 1953. Subsequent issues of *Bat Research News* focused on all aspects of bat biology but still published anecdotal and interesting band recoveries, information on band injuries, and periodic summaries of banding activities around the country. As late as 1973, the editor of *Bat Research News* (R. Martin) hoped the BBP might take the newsletter on as an affiliation, but the changing priorities of the BBP because of the moratorium on bat banding eventually precluded the affiliation (Martin, 1973b).

Banding Moratorium

The BBP issued bands to researchers until 1972. Due to overwhelming evidence of injuries and bat population declines of 22 species linked to banding-related disturbance from researchers and other causes, a moratorium on the issuing of bat bands was proposed in the fall of 1972. The bureau hosting the BBP in 1972 was the Mammal Section of the Bird and Mammal Laboratories of the U.S. Fish and Wildlife Service. The Chief of the Mammal Section, Clyde Jones, was asked to coordinate the assemblage of data on the status of populations of bats in the United States. He accomplished this by soliciting information from 100 bat researchers attending the 1970 Symposium on Bat Research. Seventy-three of the bat researchers responded with specific recommendations for bat conservation. The respondents suggested protective legislation for bats and initiation of a permitting system for bat research. A large number of respondents also identified bat-banding activities as a major source of disturbance to bats, especially in roosts. They recommended restricting the BBP in order to ease the disturbance to bat colonies. The recommendations from these bat biologists led to the following three proposals suggested by Clyde Jones in a memorandum dated September 7, 1972:

> "1. Place a moratorium of at least 5 years on issuing bat bands either to new bat banders or for new banding projects. Issue the remainder of the current supply of bat bands to investigators for use in the completion of ongoing projects that do not involve species of bats with greatly reduced populations.
>
> 2. Evaluate the bat-banding program, conduct a detailed review of the records for the recovery of pertinent biological data, and determine the feasibility of automated techniques for the program if it is to continue.
>
> 3. Take appropriate steps to effect an international treaty for the protection of North American bats similar to that established for migratory birds, and instigate legislation and corresponding regulations to activate the treaty."

These three proposals were adopted by the members of the 1972 Symposium on Bat Research, November 24–25, in San Diego, California (see Appendix 2 for a copy of the final version of the "Policy on Bat Banding and Bat Conservation"). The Mammal Section also advised the American Society of Mammalogists, the National Speleological Society, the National Parks and Conservation Association, and the Office of Endangered Species and International Activities of this policy in the fall of 1972. Members of the American Society of Mammalogists ratified the moratorium policy at their annual meeting in June 1973. In 1973, the new policy and moratorium on bat banding was published in *Bat Research News* (Martin, 1973a).

The first proposal of the policy on bat banding and bat conservation was immediately adopted as the BBP ceased to issue USFWS bat bands to researchers in 1973 (except for a few bands issued to bat banders conducting ongoing and long-term research projects). During the year the moratorium was proposed, large numbers of unused bat bands were returned by some of the major bat banders, reflecting the concern of these investigators with regard to the effects of banding on bat populations. The last set of bands sent out by the BBP appeared to be to B.J. Hayward. He was sent 300 bands on March 20, 1991, to continue a long-term banding project of Townsend's big-eared bats in the Silver City area of New Mexico.

The second proposal requested a comprehensive and detailed evaluation of the BBP, which was never completed. Past attempts were made to make the data in the BBP files more accessible to researchers and the public, but these attempts were unsuccessful due to "frustrations over the enormity of the project, inadequacies of early computers, and inconsistencies with the data" (quoted in a memorandum dated October 31, 2000, by Suzanne C. Peurach, Museum Specialist, USGS, Patuxent Wildlife Research Center, Smithsonian Institution, Washington, D.C.).

The third proposal of the bat-banding policy was to investigate taking steps to initiate an international treaty for the protection of North American bats similar to that established for migratory birds. To date, no mandate or legislation exists to protect migratory species of bats. Federal protection under the Endangered Species Act of 1973 exists for seven species or subspecies of bats in the continental United States and the sole species of bat in Hawaii (U.S. Fish and Wildlife Service, 1999; O'Shea and Bogan, 2003). Many States and territories of the United States have laws or regulations that apply to bats, but these laws tend to be in the interest of public health and address bats as vectors of disease rather than as mammals needing protection. Legislation, court decisions, and agency interpretations concerning bats also usually focus on management of bats, not conservation (Lera and Fortune, 1978). More recently, scientists convened at a workshop that addressed issues related to sampling and monitoring trends in U.S. bat populations (O'Shea and Bogan, 2003). One of the working groups at this meeting specifically identified the lack of a unifying mandate or legislative foundation for a national bat conservation program. They recommended that greater consideration be given to strengthening bat conservation efforts in the United States by the formation of official legislation and treaties (O'Shea and Bogan, 2003).

Studies using banded bats have continued since the moratorium by using privately purchased bat bands or previously issued USFWS bands, but these studies have been smaller in scale than those during the height of the BBP; smaller numbers of bats were usually banded, and study areas were more geographically localized. Banding bats is still ongoing to this day, but no official clearinghouse or program exists, nor are banding efforts coordinated in any way despite a definite need. There is also no consistency in the type of band applied to bats in current studies. A variety of band types were used after the moratorium and used to this day: lipped aluminum bands with a 2.9-mm gap made by Lambournes, Ltd., Leominster, United Kingdom (Foster and Kurta, 1999; Kurta and Murray 2002), aluminum bands made by the National Band and Tag Company, Newport, Kentucky (Bosworth, 1994; Neilson and Fenton, 1994), plastic bands made by National Band and Tag Company (Whitaker and Rissler, 1992a; 1992b), or colored plastic split-ring bands made by A.C. Hughes, Ltd., Hampton Hill, Middlesex, United Kingdom (Brack, 1983; Bain and Humphrey, 1986; Brack and others, 1991; Choate and Decher, 1996; Baptista and others, 2000; Sandel and others, 2001). A few studies used a combination of these bands (for example, Bain and Humphrey, 1986; Bosworth, 1994). A few cases of previously issued USFWS bat bands were used into the 1980s and 1990s (Goad, 1982; Brack 1983; Clark, 1984; Clark and others, 1987; Harvey, 1989; Harvey and others, 1981), and recoveries of banded bats were still being reported and published into the 21st century (for example, Navo and others, 2002).

Logistics and Data-Collection Methods

In this part, I describe the methods used by the BBP to file and keep track of banders, number and species of bats banded, information on recoveries, and any correspondence between the office, the public, and banders. In the current state of the BBP files, there are approximately 90 file drawers filled with 3×5-inch index cards of information on banded bats. There are two types of index card files maintained: one type is organized by band number and the other is organized alphabetically by bander's name. The majority of the drawers contain index cards filed by band number. Manually searching through these files by species, location, or date, is time consuming and impractical. A previous estimate of the number of individual bats banded on file range from 300,000 to 600,000 (Peurach, 2004). However, I think this estimate is low. An earlier rough estimate suggested 1.5 million bands were applied during the program up until 1968 (E.L. Davis, 1968). Additionally, in my literature review (see next section), I found that approximately 1.1 million bats were banded (table 1; Appendix 3). The actual number of index cards in the 90 drawers is unknown because not all drawers are completely full and cards vary in the number of bats they contain information for: a card could contain information on one individual bat or as many as 100 bats. For example, if every card contained information on 100 bats, and the BBP files contain information for 300,000 to 600,000 bats, the number of cards could range from 3,000 to 6,000. This is a conservative estimate of the number of cards because many cards contain information on a single bat.

Additional file drawers are devoted to bander names, contact information, and how many and what size bands were issued to each name. Each active bander had a file, which contained all of his or her correspondence with the BBP. A bander was considered "active" if he or she had banded bats within the previous 3 years. The active bander information files were kept in alphabetical order. Information on "inactive" banders was also maintained in file cabinets. I provide a list of all 107 bat banders' names compiled from the BBP files (Appendix 1).

Typically, the process by which the BBP would issue bands went as follows: the office received a letter of request for bat bands, and they then determined if the person was eligible to receive bands. The BBP then mailed the bands with a series of index cards for each bander to complete. Usually 100 index cards per 500 bands issued were sent in this shipment. Band numbers were entered at the top of the index cards, and as many as 100 consecutive numbers could be listed on the card provided that all the bats banded were the same species and sex and at the same locality. Six items were required to complete each data card: (1) band number, (2) species of bat, (3) sex of bat, (4) locality of banding, (5) bander name, and (6) date banded. The bottom of the card had three fields reserved for recovery information to be entered by staff of the BBP: (1) locality taken, (2) "by" or who found the bat or bat band, and (3) date recovered.

Bat bands were manufactured by the Gey Band and Tag Company. They were supplied as closed rings, each bearing a different number and were arranged in numerical sequence on a flexible wire (Greenhall and Paradiso, 1968). There were four different band sizes available for issue: 0, 1A, 1, 2. The No. 2 bands were the largest and most commonly used. Depending on the size of the bat band, they were numbered with either six or eight digits and have the following lettering: "WRITE F.&W. SERV. WASH. D.C. USA" or "NOTIFY NAT. MUS. FWS. WASH. D.C. 20560." No. 2 bands had both the number and the notification information on the outside of the band, whereas No. 1 and 0 had the notification information on the inside of the band (fig. 1). Up until 1953, the bands were supplied by the Bird-Banding Office at Patuxent, Maryland, to the BBP. The BBP took over the ordering of No. 2 size bands directly from the manufacturing company in the mid-1950s. Number 2 size bands were the most widely used on bats due to the evidence of injuries caused by No. 1 size bands.

When a recovery report was received by the BBP, a standard form (letter) was filled out to notify the person reporting the recovery and the original bander of the individual bat's pertinent information. Two copies were made of this letter: a copy went to the person who recovered the bat, one copy to the original bander, and the original would remain in the BBP files. The recovery information was also entered on the original index card, and a green metal tag was placed on the top of the card in the files for ease of retrieving recovery information and as a visual map of

Figure 1. Representative aluminum bands in three sizes (No. 0, 1, 2) issued by the Bat Banding Program (BBP). To the right of the bands are side views of the bands as they look when closed. Bottom side view shows the "BAT" series of band with the lipped design issued after 1953. Photograph montage created and reprinted by permission of Alfred L. Gardner.

recoveries. It was impossible to estimate the number of recoveries because not all index cards documenting recoveries had green metal tags, and multiple recoveries could be written on a card with only one green tag.

Terminology for defining different types of recoveries of banded bats was originally borrowed from the bird-banding literature and the North American Bird Banding Program (Griffin, 1940a). Griffin (1940a) defined a return as "any recapture of a banded individual at another locality, or a recapture at the same locality where it was banded, after the passage of a season when animals are believed to be migrating. If the bat has moved from one locality to another it is called a foreign return. If it is retaken at the point where it was banded after a seasonal absence, it is known as a local return." A return was also used in the homing literature to describe a bat's ability to return to its original banding site from a foreign location. A "recovery" usually meant that the banded bat was found dead. There could be "local" recoveries, which implied the banded bats were recovered dead at the original location of banding. There were also "foreign" recoveries, which were banded bats recovered in a different location than the original banding site. A recapture of a banded bat usually meant the bat was captured again in hand (using a variety of techniques) at a later date, either in the same location as the original banding or other locations. Bats were also "resighted," which usually meant the bat was not captured in hand but was seen at a close enough range to read the band number. The term "recoveries" of banded bats was often used as a catchall and could mean recaptures, dead recoveries (both local and foreign), returns, and resightings. A green tag placed on an index card could indicate that any one of these types of recoveries was reported, and the cards did not always identify the type of recovery.

Not all of the bands issued were applied to bats, and bands not used were intended to be returned to the BBP. There were approximately 69 active banders on file with the office up until 1971. From 1932 to 1951, 53 banders were on file, 33 of which were "active" (Mohr, 1952). Mohr calculated that a total of 67,279 bats were banded as of 1951, but it was not clear how many total numbers of bands were issued during that time period. As many as 107 banders were on file for the entire program, although not all were considered "active" during the entire tenure (Appendix 1). In the BBP files, I found information on number of bands issued during the following years: 1953, 5,000–10,000; 1962, 250,000; 1967, 140,000; 1968, 150,000; 1969, 160,000; 1970, 81,500; and, 1971, 56,200. Few summary statistics were available regarding bands issued and recovered, but in 1970, of the 81,500 bands issued, only 16,273 banding reports (reports indicating bands had been applied to bats) were returned to the office, 1,283 recoveries were reported, and 309 recovery form letters were written by the office. For 1971, 56,200 bands were issued, 6,255 reports were returned for bands issued, and only 312 recoveries were reported.

Because of the large number of cards and antiquated data-storage methods, searching for information on banded bats was tedious and time consuming. Solving problems, such as discrepancies in the records, also required considerable time to complete. Corresponding with bat banders and the public was slow compared to present-day modes of communication. In one file, I located a detailed handwritten account that summarized the number of banded Townsend's big-eared bats (then *Corynorhinus rafinesquii*) that probably took weeks to complete. The unwieldiness of the files led to frequent discussions of how to computerize the files as early as 1971 (Martin, 1971). As mentioned earlier, several attempts were made to enter the index cards into database management systems since 1971, but the process was never completed (Peurach, 2004). The amount of time it would take to enter all 90 drawers of cards is still a formidable task (see Access Database description in Part 2). In the late 1990s, Peurach conducted a computerization pilot study and entered approximately 3,500 records for bands issued to H.B. Hitchcock. She used Microsoft Excel to enter the records and then imported the data into Microsoft Access to run sorts, filters, and queries. She was able to run queries to identify duplicate band numbers and summarized a set of band records for big brown bats banded by Hitchcock. Her pilot study identified several problems with the USFWS bat bands, the BBP files, and recoveries, which I will summarize in a subsequent part of this report entitled “Known Problems and Case Studies.”

The BBP continues to maintain its status as a clearinghouse despite the moratorium on bat banding adopted in 1973. Recoveries continued to be reported on bats banded before the moratorium. For example, in an unpublished summary of recovery reports for 1983–84, 39 recoveries were reported and summarized by the BBP. The files are currently maintained by the USGS, Patuxent Wildlife Research Center, Biological Survey Unit at the Smithsonian Institution, National Museum of Natural History in Washington, D.C. Reports of recovered bats have become very uncommon, but the current office continues to receive reports into this century (Peurach, 2004). Unfortunately, some of these reports were for bats that had no original banding data on file (Peurach, 2004).

Knowledge Gained from Bat Banding

Bat banding led to an impressive amount of baseline knowledge of basic bat biology. The BBP’s history was fraught with problems including injuries to bats by bands, disturbance of colonies by bat banders, problems with recovery information, and errors in record keeping (see “Known Problems and Case Studies”). These problems eventually led the Bureau of Sport Fisheries and Wildlife to issue the Policy on Bat Banding and Bat Conservation in 1972, which was later ratified by the American Society of Mammalogists in 1973 (Appendix 2). However, by banding bats we learned an invaluable body of information on age estimation, behavior, dispersal, distributions, growth rates, hibernation ecology, homing, longevity, migration, movements, population estimation and dynamics, reproduction, sex ratios, survival, and swarming behavior.

Literature Survey and Summary Statistics

I reviewed and summarized the scientific literature associated with banding activities that occurred during the BBP. I began the search with references included in the library associated with the USGS Bat Population Database (BPD) library (Ellison and others, 2003; *http://www.fort.usgs.gov/Products/Data/BPD/*). I conducted additional literature searches in a number of databases, libraries, and the Internet for citations that may have been missed during the creation of the BPD. Primary sources for published banding information were in peer-reviewed journals such as *Journal of Mammalogy* and *Journal of Wildlife Management* and numerous other journals. Secondary sources were found from unpublished theses, dissertations, and a few agency reports. I specifically reviewed studies that used USFWS bands and for banding studies that occurred from 1932 until the official moratorium in 1973. For completeness, I incorporated some studies that continued past the moratorium.

I found and reviewed 173 individual publications from 139 different studies where USFWS bands were used (some authors published multiple papers on a single study). In Appendix 3, I provide a complete list of the publications I reviewed with the source citation, the purposes for banding, the dates and season during which banding occurred, the locations of the banding studies, the number of species banded and number recovered, and comments related to banding and recoveries. I further summarize Appendix 3 and provide below the total number of species banded by sex and number or recoveries, number of bats banded by geographic region, State, or country, number of bats banded by season, duration of the banding studies, and the decade their papers were published.

Thirty-six species were banded from four different bat families (Mormoopidae, Phyllostomidae, Vespertilionidae, and Molossidae) (table 1). The literature review revealed that more than one million bats were banded (1,119,141), more females than males were banded (when this was reported in the publications), and nearly 59,000 "recoveries" were reported. "Recoveries" reported in table 1 were either dead when recovered (dead recoveries), recaptures, resightings, or returns. If the study reported recaptures or resightings, this number could include multiple recaptures of the same bat. The Brazilian free-tailed bat (*Tadarida brasiliensis*) was the most frequently banded bat (590,541), followed by the little brown myotis (236,700), the gray myotis (*M. grisescens*; 82,599), the Indiana bat (*M. sodalis*; 54,904), the cave myotis (*M. velifer*; 47,054), and the big brown bat (25,505) (table 1).

Many banding studies occurred over multiple states or regions (for example, Beer, 1955; Twente, 1955a, 1955b; Hall and others, 1957; Villa and Cockrum, 1962; Myers, 1964a; Davis, R., 1966; Brenner, 1968; Easterla and Watkins, 1970; Landrum, 1971; Rogers, 1972; Mills and others, 1975; Humphrey and Cope, 1976, 1977; Tuttle 1976a, 1976b; Cope and Humphrey, 1977; Grigsby, 1980; Stevenson and Tuttle, 1981) (fig. 2). The largest number of bats banded in a State was in Oklahoma where 234,846 individuals were banded, mostly Brazilian free-tailed bats (for example, Perry, 1965; Glass, 1982). More bats were banded in the central and northeast regions of the United States than in other regions of the country (fig. 2).

Most bats were banded in the summer, but many studies also took place over multiple seasons (fig. 3). More than one-half of the total bats banded were banded in the summer months (54 percent). One-third of the total bats banded were banded over multiple seasons (35 percent), 7 percent in the winter, 2 percent in the fall, and 1 percent in the spring. Of the large number of bats banded in the summer, 97 percent were Brazilian free-tailed bats.

Duration of banding studies varied during the BBP (fig. 4). Length of banding studies was usually very short, with very few long-term attempts to follow recoveries or recaptures of banded bats. Of the 139 studies, 95 of them (68 percent) lasted 3 years or less. In many cases bats were banded at a waterhole or a day roost, and the banding site was never revisited (Cockrum, 1973). Fourteen studies occurred over 10 years or more, with four studies lasting more than 20 years. One 20-year study investigated the natural history and survival of a hibernating colony of big brown bats in a storm sewer in Minnesota (Goehring, 1954, 1958, 1972). Another long-term study banded little brown myotis, big brown bats, eastern small-footed bats, northern myotis, and eastern pipistrelles in Ontario and Quebec from 1939 to 1962 (Hitchcock, 1940, 1950, 1965; Keen and Hitchcock, 1980; Hitchcock and others, 1984). The two remaining long-term banding studies were investigations into the population dynamics of little brown bats in Indiana and Kentucky (Humphrey, 1971; Humphrey and Cope, 1976) and a long-term survival study of Indiana bats in Indiana and Kentucky (Humphrey and Cope, 1977).

Publications of bat banding studies peaked in the 1960s with 55 publications (fig. 5). Thirty-one articles were published during 1950–59 and 47 during 1970–79. The decrease in published articles in the 1970s and 1980s likely reflected the rising concern over bat-banding injuries and the concern over banding activities negatively affecting bat populations.

Table 1. Scientific name, common name, family, and species code for the 36 bats from four families referred to throughout document and in Appendix 3. North American species are listed by family in systematic order following Baker and others (2003). Also included are total number banded, number of males and females banded, and number recovered from the 173 publications (139 studies) reporting on banding activities during the Bat Banding Program (1932–72). Number of males and females banded does not always add up to the total number banded; not all publications reported number banded by sex.

Scientific name	Common name	Family	Species code	Total number banded	Males banded	Females banded	Number recovered	Percent re-covered
Mormoops megalophylla	Ghost-faced bat	Mormoopidae	MOME	24	2	22	0	0%
Pteronotus davyi[1]	Davy's naked-backed bat	Mormoopidae	PTDA	84	25	59	0	0%
P. parnellii[1]	Common mustached bat	Mormoopidae	PTPA	1,475	47	1,428	0	0%
P. personatus[1]	Wagner's mustached bat	Mormoopidae	PTPE	70	26	44	0	0%
Macrotus californicus	California leaf-nosed bat	Phyllostomidae	MACA	1,698	718	980	466	27.4%
Leptonycteris nivalis	Mexican long-nosed bat	Phyllostomidae	LENI	568	217	473	1	0.2%
Myotis austroriparius	Southeastern myotis	Vespertilionidae	MYAU	2,782	2	0	706	25.2%
M. californicus	California myotis	Vespertilionidae	MYCA	144	58	86	2	1.4%
M. ciliolabrum	Western small-footed myotis	Vespertilionidae	MYCI	42	3	4	0	0%
M. evotis	Long-eared myotis	Vespertilionidae	MYEV	213	185	28	0	0%
M. grisescens	Gray myotis	Vespertilionidae	MYGR	82,599	12,206	18,641	10,315	12.5%
M. keenii	Keen's myotis	Vespertilionidae	MYKE	1	1	0	1	100.0%
M. leibii	Eastern small-footed myotis	Vespertilionidae	MYLE	923	305	321	207	22.4%
M. lucifugus	Little brown myotis	Vespertilionidae	MYLU	236,724	16,336	13,563	19,693	8.3%
M. lucifugus/M. sodalis[2]		Vespertilionidae	MYLU/ MYSO	2,000	0	0	46	2.3%
M. nigricans[1]	Black myotis	Vespertilionidae	MYNI	134	0	0	0	0%
M. septentrionalis	Northern long-eared myotis	Vespertilionidae	MYSE	3,716	903	391	61	1.6%
M. sodalis	Indiana bat	Vespertilionidae	MYSO	54,904	10,896	13,503	9,669	17.6%
M. thysanodes	Fringed myotis	Vespertilionidae	MYTH	1,687	487	1,100	106	6.3%

M. velifer	Cave myotis	Vespertilionidae	MYVE	47,054	8,221	7,482	8,159	17.3%
M. volans	Long-legged myotis	Vespertilionidae	MYVO	396	89	237	11	3.4%
M. yumanensis	Yuma myotis	Vespertilionidae	MYYU	531	150	381	31	5.8%
Lasiurus borealis	Eastern red bat	Vespertilionidae	LABO	629	88	119	0	0%
L. cinereus	Hoary bat	Vespertilionidae	LACI	451	18	19	2	0.4%
Lasionycteris noctivagans	Silver-haired bat	Vespertilionidae	LANO	176	19	36	1	0.5%
Parastrellus hesperus[3]	Canyon bat	Vespertilionidae	PAHE	1,304	388	891	50	3.8%
Perimyotis subflavus[4]	Eastern pipistrelle	Vespertilionidae	PESU	14,545	9,654	2,842	1,631	11.2%
Eptesicus fuscus	Big brown bat	Vespertilionidae	EPFU	25,505	2,247	2,550	2,185	8.6%
Nycticeius humeralis	Evening bat	Vespertilionidae	NYHU	3,495	355	2,806	494	14.1%
Euderma maculatum	Spotted bat	Vespertilionidae	EUMA	13	4	9	0	0%
Corynorhinus rafinesquii	Rafinesque's big-eared bat	Vespertilionidae	CORA	0	0	0	0	0%
C. townsendii[5]	Townsend's big-eared bat	Vespertilionidae	COTO	4,788	462	1,638	354	7.4%
Idionycteris phyllotis	Allen's big-eared bat	Vespertilionidae	IDPH	145	18	127	53	36.5%
Antrozous pallidus	Pallid bat	Vespertilionidae	ANPA	4,273	1,145	1,398	508	11.8%
Tadarida brasiliensis	Brazilian free-tailed bat	Molossidae	TABR	590,541	44,357	121,157	4,128	0.7%
Nyctinomops femorosaccus	Pocketed free-tailed bat	Molossidae	NYFE	44	7	37	0	0%
N. macrotis	Big free-tailed bat	Molossidae	NYMA	284	10	274	0	0%
Eumops perotis	Western bonneted bat	Molossidae	EUPE	52	12	40	0	0%
Multiple species[6]				35,151	0	0	70	0.2%
			Total	1,119,141	109,661	192,686	58,950	5.3%

[1] Current taxonomy (scientific name and common name) from Wilson and Reeder (2005).

[2] Not separated out to species in text of publication.

[3] Formerly referred to as *Pipistrellus hesperus* (western pipistrelle); see Hoofer and others (2006).

[4] Formerly referred to as *Pipistrellus subflavus*; see Hoofer and others (2006).

[5] Formerly referred to as *Plecotus townsendii*; see Tumlison and Douglas (1992) and Bogdanowicz and others (1998).

[6] Number banded not specified by species in the publications.

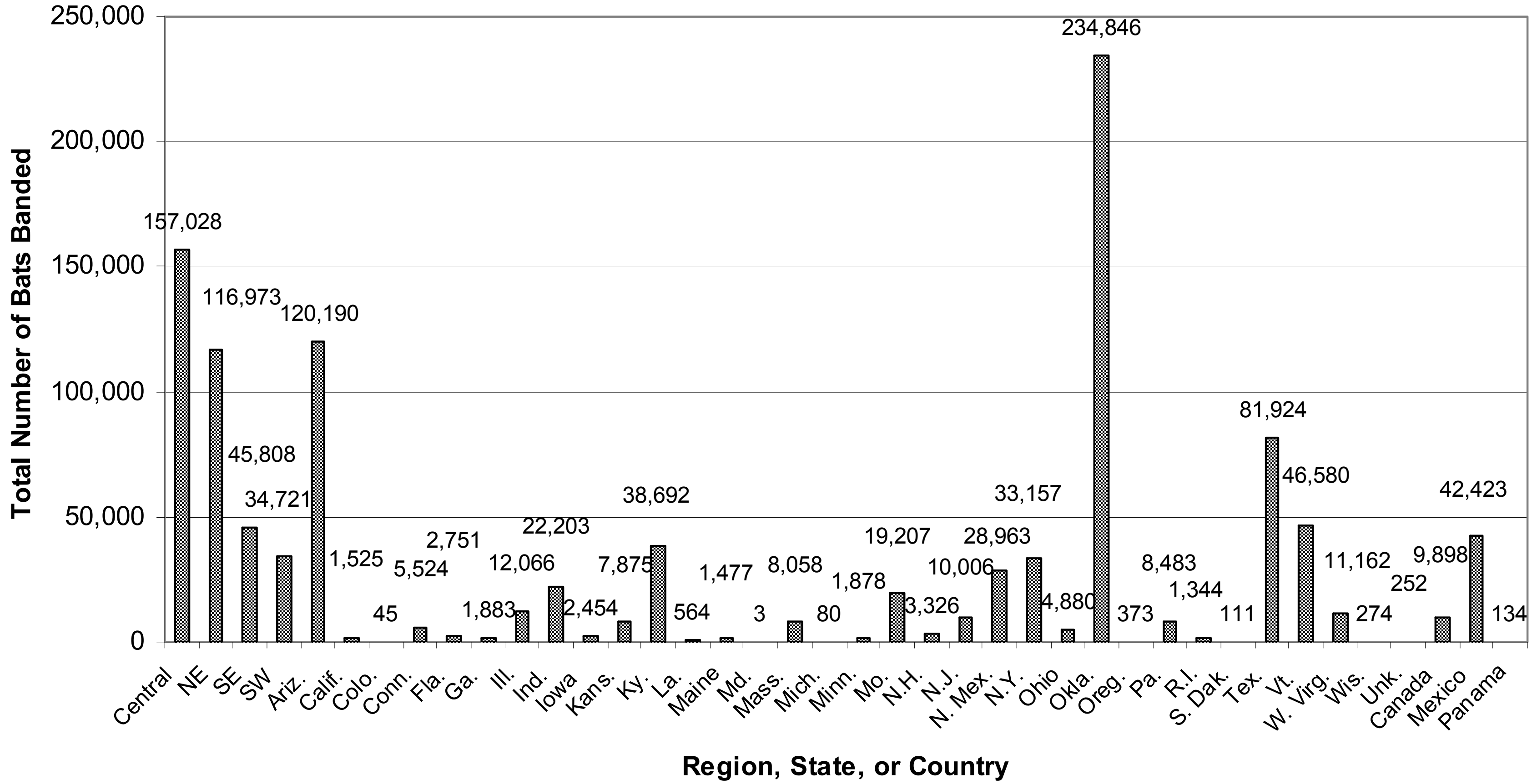


Figure 2. Total number of bats banded by geographic region, State, and country from a review of 173 publications (139 studies) related to bat banding during the Bat Banding Program (BBP) (1932–72).

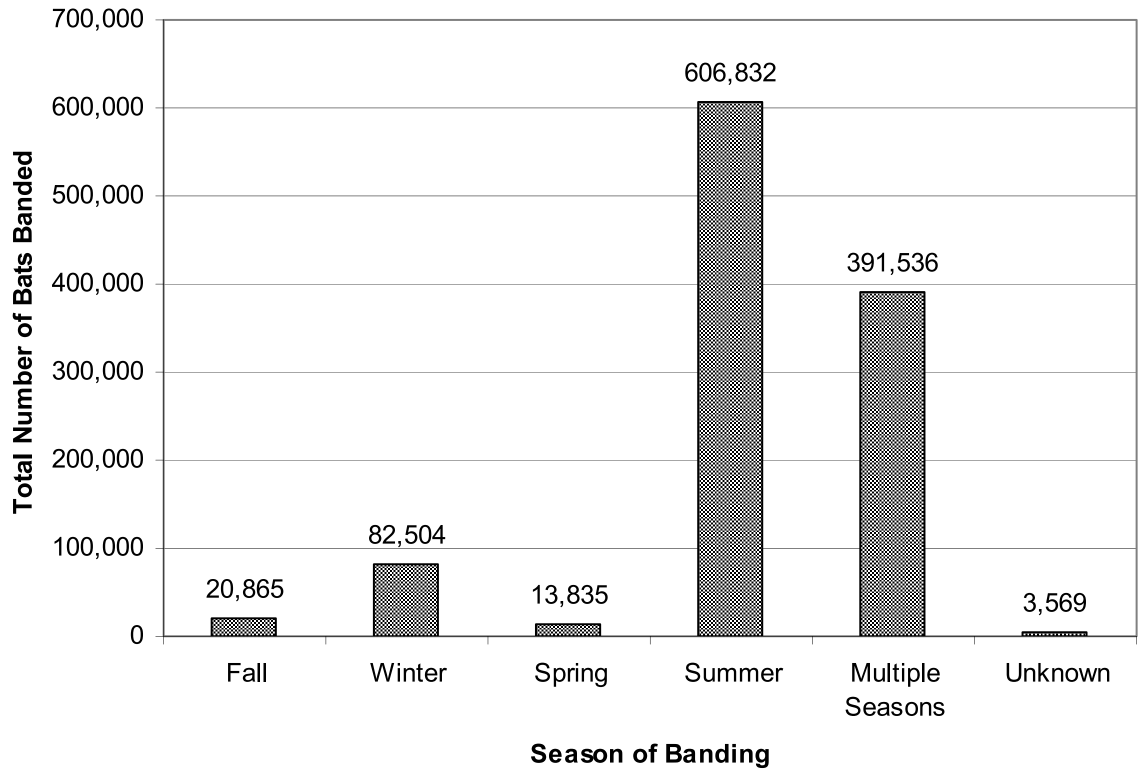


Figure 3. Total number of bats banded by season from a review of 173 publications (139 studies) related to bat banding during the Bat Banding Program (BBP) (1932–72).

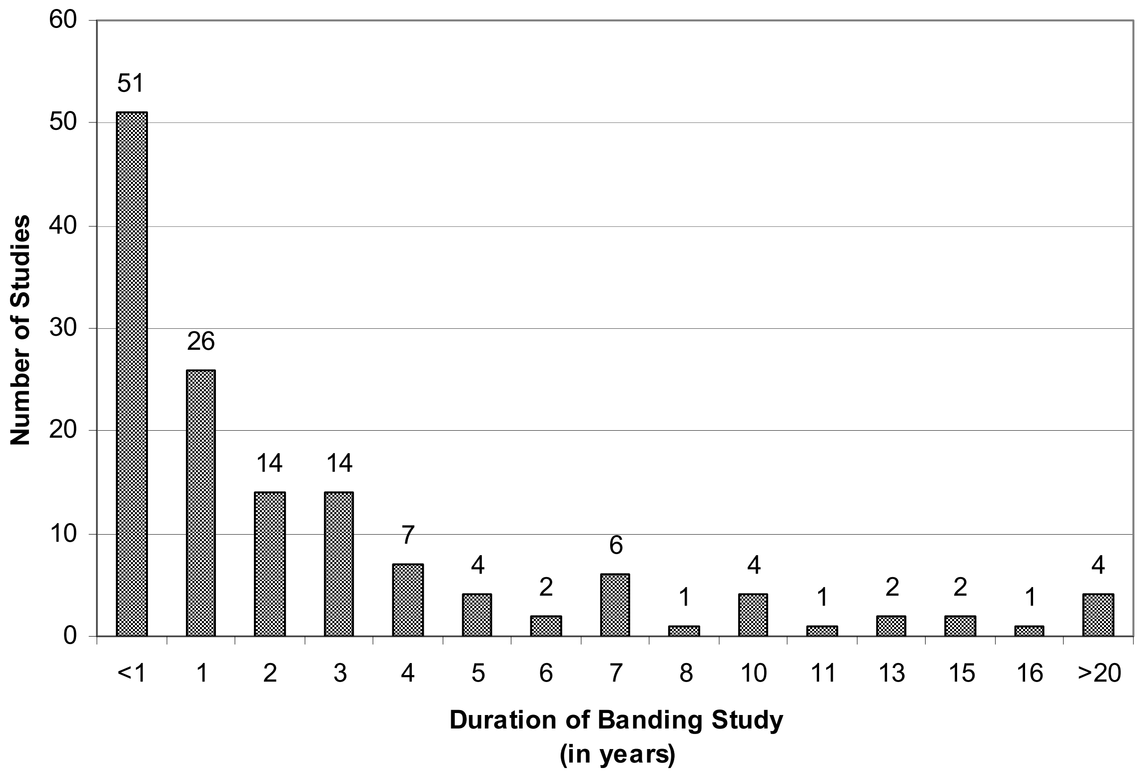


Figure 4. Duration of banding studies (in years) from a review of 139 studies (173 publications) related to bat banding produced during the Bat Banding Program (BBP) (1932–72).

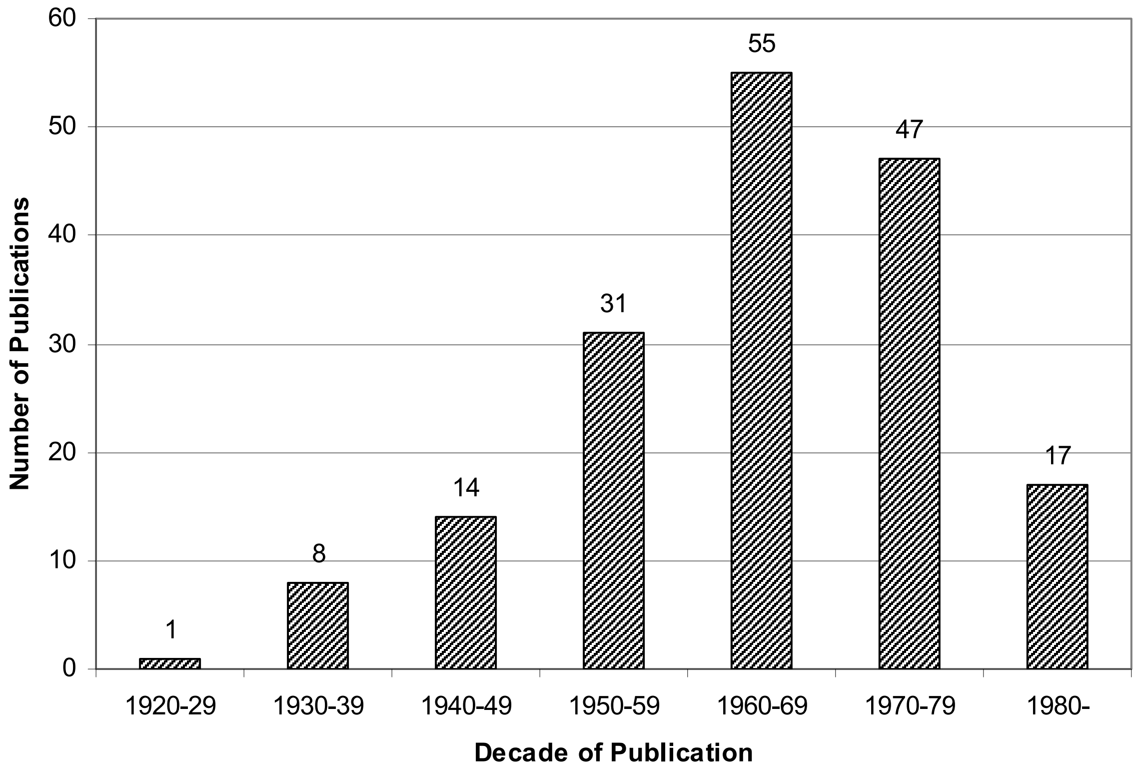


Figure 5. Number of publications by decade from a review of 173 publications (139 studies) related to bat banding during the Bat Banding Program (BBP) (1932–72).

Goals of Bat Banding

Mohr (1952) summarized the major goals of banding in the early stages of the program in his survey of bat banding in North America from 1932 to 1951. He listed the following three major goals: "(1) To determine whether the same individuals return annually to the summer roosts from which they were absent in the winter, and likewise to determine whether the same bats return in successive winters to the caves where they hibernate (migration); (2) to ascertain whether bats released at a distance from their summer roosts will return to them (homing instinct); (3) if possible, to trace the movements of individuals by recoveries of marked bats." He listed the following secondary purposes of bat banding: "(4) to determine the average and maximum length of life (longevity); (5) to determine the extent of the disproportionate sex ratios quite generally found among hibernating bats; (6) to chart growth of young bats; (7) to add to the knowledge of the life histories of various species; (8) to investigate the physiology of hibernation; (9) to trace life history of blood parasites in banded individuals; and (10) to follow the day-to-day shifts of bats within and between roosts." I found no specific publications related to Mohr's goal 9 to trace the life history of blood parasites in banded bats. The general objectives of Mohr's goals 3 and 10 to trace movements of banded bats seemed identical or at least very closely linked.

I found similar bat banding objectives in the literature with a few additions. I identified 16 unique goals or purposes for banding bats during the review of the literature during the BBP. These goals were age estimation, behavioral studies, dispersal, distributions, early banding techniques, estimation of growth rates, hibernation ecology, homing, longevity, migration, movements, population size, reproduction, sex ratios, survival, and swarming behavior (table 2). I created two additional categories for goals of banding: natural history and recovery reports. It was not always clear why bats were banded, so the broad category of "natural history" was the most frequent goal or purpose determined for a particular study (48 studies; table 2 and Appendix 3). I also used the category of natural history to describe studies that had multiple goals for banding bats, but the specific goals were not stated in the publications. I included "recovery reports" as a goal because many publications reported on interesting band recoveries anecdotally, and the recoveries were not always put into the context of a broader goal or purpose for banding (for example, longevity, migration). Many studies had multiple goals for banding bats.

Table 2. The 18 purposes of bat banding with the number of studies investigating these goals from the literature review of banding efforts during the Bat Banding Program (BBP) (1932–72).

Purpose of banding	Number of studies
Age estimation	4
Behavior	3
Dispersal	1
Distributions	1
Early banding techniques	9
Growth rates	8
Hibernation ecology	9
Homing	28
Longevity	13
Migration	11
Movements	27
Natural history	48
Population size	19
Recovery reports	18
Reproduction	9
Sex ratios	15
Survival	17
Swarming behavior	3

Below, I illustrate the invaluable knowledge we gained from banding bats during the BBP and focus on the following eight main goals or purposes: age estimation and growth rates, homing, longevity, migration, movements (local), population size, sex ratios, and survival. I combined age estimation and growth rates because these two purposes tended to be closely associated research topics. I also included a category for "other goals" not specifically illustrated in the eight main goals. For each of the topics, I give a few examples from the literature review. These examples are not meant to provide a comprehensive overview of each goal or purpose but simply provide a brief summary of how bat banding during the BBP was used to achieve knowledge about a particular topic.

Age Estimation and Growth Rates

Age estimation techniques and bat growth rates were examined using individuals banded during the BBP. Out of 139 studies (173 publications) reviewed, eight specifically investigated growth rates of bats from birth to volancy and four studies examined age-estimation techniques. R. Davis (1969) studied postnatal growth of pallid bats (*Antrozous pallidus*) in southern Arizona using known-age bats. Burnett and Kunz (1982) examined growth rates and age estimation in big brown bats from a maternity colony in Massachusetts. Pagels and Jones (1974) studied growth and development in the Brazilian free-tailed bat in Louisiana and found that bats 25 to 30 days of age could not be separated from adults on the basis of body weight alone. Kunz and Anthony (1982) studied postnatal growth and age estimation in little brown bats from maternity colonies from New Hampshire, and they developed empirical growth curves for this species that illustrated the relationships of three growth parameters (forearm length, body weight, and total gap of the epiphyses) with age. Perry (1965) and Perry and Rogers (1964) examined growth rates and age determination in Brazilian free-tailed bats.

Homing

In the early years of the BBP, many of the studies were conducted to investigate homing behavior. Of the 139 studies I examined, 28 used USFWS bands to investigate homing in bats (for example, Twente, 1955a, 1955b; Schramm, 1957; Cope and others, 1958; Hall and Davis, 1958; Gifford and Griffin, 1960; Hassell and Harvey, 1965; Barbour and others, 1966; Appendix 3). These studies typically banded bats and released them at a distance from their "home" colony. Griffin (1940a), Cockrum (1956), and R. Davis (1966) reviewed accumulated results from homing experiments conducted during the BBP. From these homing experiments, many species of bats were shown to return to their original banding site from distances of 100 miles or more, and that bats did not always appear to choose flight directions at random (Griffin, 1970). The speed and percentage of bats that returned tended to decrease with the distance the bats were transported. Most of these homing studies involved temperate zone bats that typically undergo at least short migrations at some time during their lives, even if only for short distances between summer and winter roosts (Wilson and Findley, 1972). Wilson and Findley presented a hypothetical model for homing based on randomness for the black myotis (*M. nigricans*). The black myotis forms sedentary colonies where most of the animals remain in the same location throughout the year. They found that for this particular species, homing can be explained by chance alone. General mechanisms underlying bat homing remains unresolved and equivocal even to this day (Altringham and Fenton, 2003). For short-range homing, R. Davis (1966) suggested that vision has a significant function in how bats navigate among locations. How bats use vision and other cues to navigate over long distances remain relatively unexplored to this day.

Longevity

Bat banding during the BBP provided longevity records for many species in North America. Cockrum (1956, 1973) and Paradiso and Greenhall (1967) summarized longevity records for various species of bats banded with USFWS bat bands. None of the bats banded were of known age, so we can only assume a minimum age for all of these longevity records. The oldest banded bat on record in the BBP records was a little brown myotis that was banded in an iron mine in New York in 1961 and was recaptured in the winter of 1995, making it at least 34 years old (Davis and Hitchcock, 1995). Since 1995, this record has been exceeded by a Brandt's bat (*Myotis brandtii*) banded with an aluminum forearm band and recaptured 41 years later in Siberia, Russia (Podlutsky and others, 2005). For little brown bats in North America, records exist for this species living 10, 11, 12, 13, 14, 20, 23, 29, 30, and 33 years (Cockrum, 1956; Davis, 1982; Bowles, 1983; Sommers and others, 1993; Davis and Hitchcock, 1994). There were records of big brown bats living to be 8, 9, 19, and 20 years old (Cockrum, 1956; Paradiso and Greenhall, 1967; Davis, 1986), Indiana bats living to be 10 and 13 years old (Cockrum, 1956; Paradiso and Greenhall, 1967), Townsend's big-eared bats, 16 and 21 years (Paradiso and Greenhall, 1967; Perkins, 1994), and eastern pipistrelles, 11 years (Paradiso and Greenhall, 1967). Thirteen of the studies examined during the literature review specifically examined longevity or reported on noteworthy longevity records of banded bats.

Migration

The banding of bats during the BBP revealed our first glimpses of how seasonal migrations are an important life-history strategy for several species of bats. Of the 139 studies I reviewed, 11 examined migration patterns of bats using banded individuals. Migration is a seasonal, usually two-way, movement from one place or habitat to another to avoid unfavorable climatic conditions or to seek more favorable energetic conditions (Fleming and Eby, 2003). Recoveries of banded bats in the New England States by Griffin (1940a, 1940b, 1945), Gifford and Griffin (1960), and Davis and Hitchcock (1965) showed that little brown bats predominantly migrated southeast in the spring and northwest in the fall with up to 150–170 miles between summer and winter locations (Griffin, 1970). In the Midwest, recoveries of banded bats demonstrated seasonal migration of little brown bats and Indiana bats from hibernacula in Kentucky northward to summer colonies in Indiana, Ohio, and Michigan. These bats sometimes migrated as much as 350 miles (Hall, 1962; Humphrey and Cope, 1963; Hassell and Harvey, 1965; Barbour and Davis, 1969). Gray myotis were shown to migrate for considerable distances between caves and summer colonies in Kentucky and Tennessee (Hall and Wilson, 1966). The most frequently banded species during the BBP was the Brazilian free-tailed bat. Band recoveries of free-tailed bats painted a picture of seasonal migrations that commonly extended into Mexico and involved movements of as much as 800 miles. A Brazilian free-tailed bat originally banded at Carlsbad Caverns was recovered 800 miles away by Villa and Cockrum (1962) in central Mexico. Additional recoveries corroborated these long- distance migrations. The work of Eads and others (1955), Short and others (1960), and Davis and others (1962) demonstrated movements among Texas caves up to 170 miles and 400-mile movements from Texas caves to Carlsbad Caverns. Fall migrations of as much as 500 miles southward from Oklahoma to Texas were demonstrated by Glass (1958, 1959, and 1982). An excellent summary of bat banding in the context of migration can be found in Baker (1978).

Movements

More localized movements of bats were also studied with the use of banded bats during the BBP. Twenty-seven of the studies reviewed examined movements. Early banding revealed that bats frequently switch among a series of roosts (both in winter hibernacula and in summer roosts). Additionally, bats can move their locations within a particular roost. Baker (1965) found that banded eastern pipistrelles hibernating in caves in Georgia moved up to 65 miles to other caves during the same winter. Similarly, banded big brown bats in Minnesota were observed to move from one cave to another during the winter (Beer, 1955). In Arizona, Brazilian free-tailed bats were found to move among "multi-use" roosts during the summers (Cockrum, 1969). Banding studies also revealed that canyon bats have little fidelity to a particular crevice from day to day during the summer, but many individuals of this species would remain in a general roost area (Cross, 1965). Grigsby (1980) found that banded gray myotis bats in northeastern Oklahoma exhibited considerable movement between caves following the maternity period and prior to migration to their hibernacula. Movements could also occur within a cave especially for those species that formed clusters. Movements of this type were documented for Indiana bats (Hall, 1962) and cave bats (Twente, 1955a, 1955b; Tinkle and Patterson, 1965).

Population Size

Nineteen of the 139 studies I reviewed estimated population size or abundance of bats. Of these, only six used banded bats and mark-recapture techniques to estimate abundance. The remainder of the studies used visual counts such as emergence (flight) counts (for example, Mills and others, 1975; Humphrey and Cope, 1976), counting individuals within a roost (for example, Mumford, 1958; Humphrey and Kunz, 1976; Cockrum and others, 1996), and total area estimate techniques where the number of bats within a cluster was estimated and then extrapolated across the entire roosting area (Dunnigan and Fitch, 1967; Easterla, 1973). Kunz (1973) used a variety of techniques to estimate the population size of cave bats in south-central Kansas. In addition to flight counts from roosts, he used a combination of the following techniques: the size of the stained area within the roosts, the quantity of guano within the roosts, number of neonates present after adults had left the roost, and total area of roost covered by clustering bats. Of the six studies estimating population size using mark-recapture techniques, the majority used the Lincoln-Petersen method (Tinkle and Milstead, 1960; Phillips, 1966; Constantine, 1967; LaVal, 1973b). The Lincoln-Petersen method, also called the Lincoln Index, provides an estimate of population size based on the ratio of recaptured marked animals to unmarked animals (Pollock and others, 1990). This estimator is based on the assumption of equal catchability of the animals in the population, which is unlikely to be true in many wild populations and could lead to biased estimates of the population size. Brenner (1968, 1974) used mark-recapture data to estimate population sizes of big brown bats and little brown myotis, respectively, but he did not describe the analysis technique he used.

Sex Ratios

Banding studies revealed early information on disproportionate sex ratios in summer roosting and winter hibernating bats. This was well documented in the bat-banding literature (Davis, 1959; Barbour and Davis, 1969; Humphrey and Kunz, 1976). Of the 173 publications I examined, 15 studies examined sex ratios in banded bats. Davis (1959) found that 80 percent of cave-hibernating eastern pipistrelles in West Virginia were males and speculated this was due to differential survival between the sexes and probable differences in roosting behavior and geographic location of roosting between males and females (more females were roosting farther south than males). Humphrey and Kunz (1976) found more female than male Townsend's big-eared bats in hibernacula in Kansas during the winter months and attributed this to sex-specific winter behaviors. Pearson and others (1952) speculated that disproportionate sex ratios in winter were due to winter foraging activity and the use of alternative roost types by males and females. Smith (1957) examined sex ratios in the little brown bat and found that although equal numbers of males and females were born, the number of males decreased steadily during the summer and autumn, a common occurrence for many species that form maternity colonies.

Survival

Early studies examining survival in bats were conducted during the BBP. Of the 139 studies reviewed, 17 specifically addressed survival using USFWS banded bats. O'Shea and others (2004) summarized and critically appraised the various techniques used to estimate survival from banded bats using several examples from studies occurring during the BBP. For example, Beer (1955) used life tables to estimate survival in big brown bats in Minnesota and Wisconsin and estimated an overall rate of mortality of 40 percent with survival lowest in the first year. Pearson and others (1952) examined population dynamics in Townsend's big-eared bats in California and used descriptive techniques to estimate a 40–54 percent return for juveniles after one year with 70–80 percent return rate for adult females. Goehring (1972) studied big brown bats in Minnesota and estimated 60 percent survival for the first year after banding with a higher rate thereafter using descriptive techniques from band returns. Elder and Gunier (1981) examined survival in gray myotis in Missouri from 1968 to 1978 and found male annual survival to be 70 percent and female 73 percent with lower rates for the first year. Stevenson and Tuttle (1981) also studied survival in gray myotis, but in Alabama and Tennessee from 1968 to 1976 and found survival to be similar by sex, with first-year survival highly variable (0.06–0.73), whereas after first-year survival was higher (0.57–0.85). Humphrey and Cope (1976) studied survival in little brown bats in Indiana and Kentucky and found that survival in the first year after banding ranged from 13 to 49 percent with survival rates in subsequent years being 54–86 percent. All of these early studies used ad hoc, descriptive methods to estimate survival and rarely provided estimates of variances (O'Shea and others, 2004). Two analyses of survival based on Hitchcock's long-term banding effort from 1941 to 1962 (with searches for banded bats continuing into the 1980s) in Ontario were the first publications to use the maximum-likelihood-based Cormack-Jolly-Seber (CJS) model to estimate survival in bats (Keen and Hitchcock, 1980; Hitchcock and others, 1984). The theory behind mark-recapture analyses has evolved substantially since the early days of banding bats (see Lebreton and others, 1992; Williams and others, 2002; Amstrup and others, 2005). I further discuss mark-recapture techniques and the biological parameters that can be estimated using marked bats in Part 2.

Other Goals

Other goals or purposes for banding bats gleaned from publications that were not specifically illustrated previously were behavior, dispersal, early banding techniques, hibernation ecology, recovery reports, reproduction, and swarming behavior. Studies that looked at aspects of bat behavior related to site fidelity included Rice (1957) and Tinkle and Patterson (1965). Davis and others (1968) examined banded big brown bats and colonial behavior in Kentucky. Dispersal of bats was studied by Phillips (1966) and Bateman and Vaughan (1974). Many early banding studies focused on banding techniques and were reviewed more thoroughly in the "History of Bat Banding" part above. Banding bats at hibernacula revealed much about the ecology of hibernating bats during the winter months. Three publications specifically focused on "hibernation ecology" as their purpose in banding individual bats. These studies were Folk (1940), Davis and Hitchcock (1964), and Tinkle and Patterson (1965). Incidental and interesting recovery reports were published in 17 cases usually related to longevity. Patterns of reproduction were specifically studied in four publications (Pearson and others, 1952; Short, 1961; Brenner, 1968; Kunz, 1971b, 1974); however, many other publications reported studies on reproduction as secondary objectives. Swarming behavior was examined by Davis (1964b) and Cope and Humphrey (1977).

Problems with the Bat-Banding Literature

In my review of the literature on banding studies published during the time of the BBP, several problems were revealed. These problems were mostly due to a lack of documentation and unclear methods. Often it was unclear how many bats were banded, how many were banded by species, and sex or age ratios of bats banded. These basic statistics were not always reported (for example, Beer, 1955; Davis, 1957; Myers 1964a). Frequently, a total number of bats banded of multiple species was cited in text, but the number of bands applied to each species was never clarified (for example, Griffin, 1945; Barbour, 1950). Of the 139 banding studies reviewed, eight studies reported on banding multiple species but did not state how many bands were applied to a particular species (Appendix 3). For example, in a study of swarming behavior, Davis (1964b) banded more than 12,000 bats (of multiple species) during 17 days in the fall but did not separate the number banded by species. Recoveries and recaptures were not always reported in the publication to species or sex. Of the 139 studies reviewed, 46 of them did not report number of recoveries. Either the recoveries were not stated or reported in text, were not reported to species or sex, or were not clearly summarized in the text of the publication (Appendix 3). Cockrum and others (1996) provided the most detailed accounts of recoveries by location found (Appendix 3). The authors included detailed information on where and when bats were banded and if they were recovered.

Another problem I encountered while reviewing the literature was a lack of clarity in the terminology of recoveries reported. As mentioned earlier, the terminology for defining different types of recoveries of banded bats was originally borrowed from the bird-banding literature and the North American Bird Banding Program (Griffin, 1940a). The term "recoveries" of banded bats commonly was used as a catchall and could mean recaptures, dead recoveries (both local and foreign), returns, and resightings. The types of recoveries reported often were not explicitly stated in publications.

I also found many studies where it was not always clear which type of marking technique was used. For example, while reviewing Mohr's banding efforts in Pennsylvania in the 1930s, it was impossible to tell how many bats were "marked" with bands versus "tagged" with fingerling ear tags. He also never reported on number of bats banded by sex, nor did he report the sex ratio of recovered bats (Appendix 3). Another example involved publications by Clark (1984) and Clark and others (1987). They reported in their methods that they used a combination of USFWS bands and plastic split-ring bands (A.C. Hughes), but they gave no indication of which species received which type of band (Appendix 3). A few publications simply did not state what type of band was applied to the bats, but I made an assumption they used USFWS bands because of the date of the publication and because the banders' names were found in the BBP files (that is, Cockrum, 1952; Davis and Cockrum, 1962, 1963). Cope and others (1961a) described a method to tag bats using USFWS bands coated with radioactive Gold-198, but they did not state how many bats were banded using this method in the paper.

Cross-referencing information among different publications was time consuming, difficult, and often led to dead ends. Griffin (1945) banded 13,000 bats of six species from 1934 to 1940, but in another paper describing the same study and location, he reported 11,739 bats of six species were banded. Patterson (1961), Tinkle and Milstead (1960), and Tinkle and Patterson (1965) banded cave bats in Texas in the late 1950s to early 1960s, and it was difficult to discern the overlap among these three studies in terms of how many bats were banded and how many recoveries compared to recaptures were reported. Some papers would describe banding bats, but as part of another study. For instance, Girard and others (1965) studied rabies in bats in New England. The authors stated that "most of the bats captured were banded and released for further study of bat ranging and seasonal migration" but did not provide any details on number of bats banded, the types of bands used, or recovery/recapture rates.

In general, recovery and recapture rates reported in the literature were low (table 1 and Appendix 3). Barbour (1950) recorded low recoveries for bats banded by Welter and Sollberger (1939) from Bat Cave in Kentucky. Of 2,000 little brown bats and Indiana bats banded there in April, 1937, only 70 were found there in November 1937, 6 were found in February 1939, 27 in November 1939, and 13 on March 15, 1941. In 1945, no banded bats were found, and during each followup survey, no banded bats were "recovered" more than once. Cockrum (1969) studied migration of Brazilian free-tailed bats and summarized "in-place" recoveries (local recoveries) for Eagle Creek Cave in Arizona. In the same year, rate of recovery for both females and males never exceeded 2.4 percent. Recovery rates declined 1, 2, and 3 years after banding. By the third year after banding, the recovery rate for females was 0.01 percent and for males, 0.18 percent. I calculated a rough estimate of an overall "recovery rate" of 5.3 percent across species and locations from table 1. This number was in no way an estimate of a capture probability for all bat species because there was no control for sampling effort, and recoveries were a combination of four different types (dead recoveries, recaptures, returns, and resightings). The percentage recovered was calculated to simply give a rough idea of the number of bats seen again at least once after banding. Twelve of the species banded were never recovered. For bats recovered at least once after banding, the percentage recovered ranged from a low of 0.2 percent for the Mexican long-nosed bat to a high of 36.6 percent for Allen's big-eared bat (table 1). A single Keen's myotis was banded and recovered (100.0 percent recovery) in a homing experiment conducted by R. Davis (1966) and Davis and Cockrum (1962).

Known Problems and Case Studies

In this subsection I describe in detail the three main reasons for the moratorium on bat banding of 1973: (1) problems related to the bands themselves such as direct injuries to bats and illegibility of the numbers on the bands; (2) disturbance of bats at roosts during banding activities; and, (3) problems with the BBP files themselves and the validity and quantity of recoveries, recaptures, or resightings of banded bats. I illustrate these problems with specific case studies either from unpublished memoranda located in the BBP correspondence files, other unpublished correspondence files, personal communication with bat banders, and the published literature. Evidence of band injuries and disturbance to bat roosts was not always published, and the only records for this information exist in memoranda buried in the BBP files and individual researcher's files.

(1) Problems with Bands

Two major problems with USFWS bands confronted the BBP during its entire tenure: direct injuries to bats from the bands and eventual illegibility of the bands after application. Both of these problems seriously compromised the reliability of recoveries and recaptures of banded bats. Because of these two problems, the BBP coordinated the experimentation and testing of different styles of aluminum bands applied to bats during the entire program; however, testing of different types of bat bands was especially prominent in the 1960s. Other researchers were experimenting with new designs and other types of bat bands outside of the BBP with private funds in the 1960s to early 1970s (that is, Hitchcock and plastic split-ring bands), but much of this research was anecdotal and sporadically published and therefore not easily accessible.

Direct injuries to bats from the application of USFWS bands were common in early years (pre-1955) with the use of bird bands and also in later years with the specially designed bat bands introduced in the mid-1950s. The sharp metal edges of bird bands, especially at the corners, were found often to cut into the wing membranes of bats causing flesh to grow over the ends of the band (Trapido and Crowe, 1946; Cockrum, 1956; Hitchcock, 1957). The resulting irritation was therefore more likely to cause the bats to chew on the bands, which then made them illegible. In a letter to Hitchcock (1957), R.B. Davis wrote that he had examined 190 Brazilian free-tailed bats one month after they had been banded and found that 86 showed no irritation or swelling, 104 were injured, and 33 of the injured bats were so badly injured that he sacrificed them. Other researchers banding Brazilian free-tailed bats experienced similar problems. The evidence of injuries and even death to bats from these bird bands was the impetus for developing a new “lipped” (also called “flanged”) band based on a Dutch design. It was also recommended that the corners of the bands be rounded by the bander by filing them down before application to the bats. The lip-end type bands were issued by the BBP beginning in the mid-1950s until the moratorium in 1973, but not to all banders (straight-edged bands were also issued until the end of the BBP). Development of these new bat bands did not solve the problem of injuries and illegibility. Herreid and others (1960) studied band injuries and survival in Brazilian free-tailed bats from 1956 to 1959 and quantitatively compared the injuries caused by the two types of bands (bird bands and the new bat band [series 10-00001 to 10-40000]). The new bands caused injury at a slower rate than bird bands; however, the percentage of “good bands” in the field was about the same for both types of bands at 181–300- and 361–730-day intervals after application. The two types of bands caused different injuries with the bat bands causing fewer embedded injuries than the bird bands but causing more wing tears. Perry and Beckett (1966) banded neonatal Brazilian free-tailed bats with two different sizes of USFWS bands: 400 bats were banded with No. 1 size and the remainder with No. 2 bands. The group banded with No. 1 size bands showed great frequency and severity of band injury compared to the larger No. 2 bands. The small bands even caused skeletal damage to the developing bones of the forearm and manus.

The seriousness and degree of injuries seen by bat banders appeared to differ depending on the bat species (Humphrey and Kunz, 1976). There was evidence that Townsend’s big-eared bats were especially prone to injuries from bands. Humphrey and Kunz (1976) quoted that this species responded “more strongly than has any other temperate zone species on which we have conducted capture-recapture studies.” Problems included in-grown bands, chewed bands so that they could not be read, and infected forearms. Some bats exhibited all three problems at once. Humphrey and Kunz (1976) did not see direct mortality from bands, but they suggested that this species should not be banded unless important new capture-recapture data were needed. If banding were to continue with Townsend’s big-eared bats, they suggested slitting the wing membrane and closing the band through the hole, as is necessary with many tropical species that react in a similar manner. The cave myotis, on the other had, did not seem to incur many direct injuries from USFWS bat bands (Patterson 1961; Tinkle and Patterson, 1965).

Correspondence and articles included in the early issues of *Bat Banding News* provided much of the information on band injuries and the concern many of the banders felt about these injuries to survival of bats in the wild. The search for a less injurious and more legible bat band was an ongoing effort during the 1960s. Mueller (1961) wrote about banding eight big brown bats with the new “lipped” bat band; he kept these bats captive for a period of 6 weeks to several months. Several of the bats developed band injuries, and in two cases the injuries were so severe as to prevent flight. He stated these bats would not have survived in the wild. Bell (1961) also wrote that he became “discouraged because of injuries to the wings, but by the flat-lipped bands.” In this same issue of *Bat Banding News*, the editor W.H. Davis announced the appearance of yet another “New Bat Band,” a band that clips to the wing and clinches upon itself like a paper staple (Davis 1961a). He applied 100 of these new bands to little brown myotis in November of 1960. He returned to the same site in spring 1961 and "nearly all these bats were retaken and none had injury or chewing," but he felt that it would be necessary to have the bats "drag their tags through the buildings for a summer" before drawing any major conclusions. In a later issue, he stated that the bands with the experimental clip cut through the wing membrane causing serious injury (1961d). With the standard type No. 1 bird bands on little brown myotis, serious injury, chewing, or both was almost 100 percent (Davis, 1961b). Later in the same year, Davis concluded that No. 1 bird bands should not be used on bats with the exception of the canyon bat and the California myotis.

Testing of different band types continued into 1962 (Davis, 1962a, 1962c). Two different styles of No. 2 bands were tested, one lipped and the other with the corners rounded off. Both were made to specifications by the Gey Band and Tag Company. The band with the rounded ends was "very promising" (Davis, 1962a). No injuries to bats were seen with this band, but some were still chewed by the bats and therefore eventually became illegible, defeating the purpose of banding. Degree of chewing of bands as well as injuries appeared to vary in severity depending on the bat species and individual behavior of the bats. If a band number was unreadable, the original banding information on species, date, and location was completely lost. As an example, a banded bat was found at Edwards Ferry, south of Pooleville, Maryland, and sent to the BBP, but the band was so badly chewed, the number could not be read (Davis, 1962c). Cockrum (1969) speculated that many of the bats he banded from 1952 to 1967 chewed on newly applied bands enough to actually remove the bands. He further stated that "guano bats appear to be much more aggressive and persistent in their attempts to remove bands than are other species banded in southern Arizona, although some *Eptesicus fuscus* [big brown bats] and *Myotis velifer* [cave myotis] and a few *Macrotus waterhousii* [now *Macrotus californicus* (California leaf-nosed bat)] also chewed bands extensively." Bonaccorso and Smythe (1972) also reported injuries and band illegibility due to chewing. They reported that on numerous occasions they had recaptured bats, "sometimes within hours of banding, only to discover the band already badly damaged." They also corroborated with other banders in that the frequency of "band-chewing" varied by species, "with bats of the genera *Carollia*, *Artibeus*, and *Desmodus* particularly apt to chew bands." In their experiences, bands also caused injuries to the forearm and wing membrane as described by Herreid and others (1960).

Methods by which bands were applied could make a difference in the level of injury incurred by bats and how well the bands could be subsequently read. Trapido and Crowe (1946) found this inadvertently when they closed bands more loosely and allowed the band to slide along the forearm of the bats. The authors reported that this seemed to cause no discomfort, bats made no attempt to chew on the bands, and these bands were found to be clearly legible without a scratch after several years. Irritation and eventual injury also occurred due to improperly opened bands prior to placing on the bat, resulting in uneven closure of the band on the bat's wing. Bands were issued by the manufacturer as closed rings on a flexible wire. Prior to applying the bands to bats, these rings needed to be opened manually. If the bat bands were opened unevenly, they could not be closed evenly, and this caused pinching of the wing (Davis, 1961c; Elder and Gunier, 1972). However, even when bands were well applied, injuries due to bands and eventual illegibility continued (Cockrum, 1969). Brazilian free-tailed bats chewed at well-applied bands, and chewing was especially noticeable with the smaller bands (No. 0) (Cockrum, 1969).

In 1963, *Bat Banding News* discussed the idea of color anodizing the bat bands to help with long-term legibility (Davis, 1963). However, anodizing No. 2 size bat bands made it much more difficult to open the bands prior to applying to the bats, so W.H. Davis wrote to both the Gey Band and Tag Company and the BBP about the possibility of obtaining bands with legible numbers, pre-rounded edges, preopened, and in a choice of four colors. He believed that bands made with a harder alloy would be better because bats were less likely to be able to chew the band and render them illegible. In a note in *Bat Research News*, W.H. Davis described information on the British

Lambournes bat band, a 4-mm-diameter-style bat band, which was the same size as the No. 2 bands used in the BBP (Davis, 1965). He reported they were made of a special alloy much harder than the aluminum used by the BBP that was resistant to chewing by bats. He further noted that the No. 2 bands in the "642" series were so hard that it appeared to solve the chewing problem.

In 1966, it was announced that yet another new bat band was available (Davis, 1966a). The new bands were No. 2 size with small lips and numbers that began with a "BAT5" prefix. However, the quality of the workmanship was disappointing to W.H. Davis. The numbers were "still" sloppy, and the flat-topped 9 "still" looked like a 5. This had led to many errors in reporting in the past, particularly by the public who were not familiar with the band. In a subsequent issue of that same year, use of these new bands was discontinued because in order to be made "lipped" they had to be made of a soft alloy and hence were too soft to be used on bats. The quest still continued to find the perfect bat band (Davis, 1966c). In this same issue, M.B. Fenton also reported that this new series of BAT5 bands were too soft to be used on bats. He found that bands from this series were being chewed to illegibility within a matter of weeks after they were applied to bats.

The following year, A.M. Greenhall, who at the time was in charge of the BBP announced that his office would like to cooperate with bat banders in creating the type of band needed for bats (Davis, 1967a). He needed agreement with the current banders on what they wanted before asking for further funding to create the proper band. The list of most important features collated by W.H. Davis was (1) legibility, (2) legend on the outside, (3) hard enough that it is not easily chewed, (4) ends rounded and smooth, and (5) the bands open with a gap of about 2 mm and are strung in groups of 100 on plastic tubing. In June 1967, bat banders met at the annual meeting of the American Society of Mammalogists to discuss problems concerning bands used on bats. After considerable discussion, several recommendations were passed without dissent. It was recommended that the BBP should supply "rounded end" bat bands with the metal as hard as practical, and they were further urged to budget for more experimental types of bands and tags for bats (Davis, 1967b). However, through 1969 the office was still issuing the soft-lipped bands because they were the only ones available (Davis, 1969a). In a memorandum written by William H. Elder, a bat bander, dated August 7, 1970, he complained about USFWS bands still being issued to banders that were so soft that they were "easily chewed away by bats and thereby give entirely different population turnover rates from one decade or one species to another." Apparently, the softness of the alloy used to create bands was also a problem for the Bird-Banding Office because legibility of band numbers was not lasting for long enough periods of time. Elder suggested in his memorandum that the metal for all bands applied to birds and bats should be submitted to the Bureau of Standards prior to accepting it for purchase. He further stated that "some of the old, hard bands from 10 years ago that were carefully applied are still as legible as ever."

As late as 1970, it appeared that many banders were also still using square-cornered bat bands instead of the recommended "rounded end" bat bands. H.B. Hitchcock reiterated that the "square-cornered bat bands are bad" in a memorandum dated December 30, 1970. The corners should be rounded by bat banders by filing them down before applying them to bats. He also said that the band edges should be rounded as well as the corners and he suggested this could be done by the manufacturer of the bands. He was accompanied by a Dutch bat bander, P. Bels, to one of his study sites where they recaptured many previously banded bats, many of which had bands imbedded and partly overgrown. P. Bels was "shocked to see this and said that if such injuries happened in his country he would fear action would be taken against him."

Even toward the end of the BBP, the system of numbering and style of the bat bands continued to be a topic of concern. Clyde Jones, the Chief of the Mammal Section of the Bird and Mammal Laboratories, U.S. Fish and Wildlife Service, wrote in a memorandum dated June 2, 1971, that "the system of numbering and style of the bats bands should be modified." For the most commonly used No. 2 bat band, both the interior and exterior surface was stamped with the notification information (see fig. 1), but the band number was only on the exterior surface. He wrote that the band number should be on both sides of the bands. He also suggested the bands should be made from a "slightly harder metal; this would result in reduced distortion of numbers from being chewed by bats and thus reduce the errors in reading identification numbers on banded bats." In 1972, Elder and Gunier (1972) published information on improved tools for bat banders, but by that fall the new policy on bat banding was discussed at the third annual meeting of the North American Symposium on Bat Research was held in San Diego, California (November 24–25, 1972).

Reliable information gained from banded bats was not only compromised by band injuries and unreadable numbers on the bands, but there could also be difficulty retrieving band information due to roost characteristics. For example, Cope and others (1961a, 1961b) used a radioactive labeling technique on the USFWS bands applied to big brown bats and little brown bats in building colonies in Indiana. The radioactive coating on the bands made the band detectable through a 2-inch thickness of wood, tin, brick, and slate, and enabled the authors to record high percentages of returns (or recaptures) when bats were completely hidden from view and not catchable. In one building, they saw only two banded bats, but yet they were able to determine 80–90 percent of the 40 originally banded bats had returned to the same roosts (they were released earlier that same night 20 miles away for a homing experiment). This technique had drawbacks in that the effects of the radioactive labeling on the health of the bats were unknown, and the individual band numbers could not be determined.

Bands did not necessarily stay on bats, and identification numbers on the bat bands would become unreadable due to other variables besides chewing by bats. Bergstrom (1978) reported finding seven USFWS bat bands on the floor of a cave with a hibernating colony of Indiana bats (*Myotis sodalis*) 13 years after M.B. Fenton had banded them. Two of the bands could not be read because they were chewed on by what was presumed to be predators (members of the weasel family). The bat bands could also have their numbers obliterated simply by the characteristics of the roost the bats inhabited and scraping movement in and out of the roost.

Injuries to bats from banding were not unique to the USFWS style aluminum bands used during the BBP. For example, Edith Bragg described injuries she witnessed to Townsend's big-eared bats in Idaho in a memorandum to Clyde Jones of the BBP dated January 23, 1973. She described a program of banding this species with split-ring celluloid bird bands similar to those used by Hassell (1967). She wrote,

> "Few bats seemed to notice these bands, but those that tried were able to remove the bands within five minutes. All animals were banded during the hibernation cycle, and no ill effects were noted through the first year. During the second year, however, many females hibernating in the mines were noticed to have suffered banding injuries. Apparently, the heat in the nursery colonies caused band irritation in the females, while the males that remained in cooler places appear unaffected. The females chewed the bands until the membranes were pierced and many bands rotated. Many have tissue that has grown over the band, but others still have injuries that have not really healed."

Pierson and Fellers (1993) reported on injuries to more than 11 percent of Townsend's big-eared bats in California banded with 3-mm lipped bands (Lambournes Ltd., England). In a letter to the editor of *Bat Research News* in 1994, P. Richardson described injuries using Lambournes bat bands on Daubenton's myotis (*Myotis daubentonii*). He noticed damage caused by the bands, but that the damage was variable in that some individuals "have been carrying the bands for 12 years and show no ill effects, others wear them for a few weeks and a hole has developed through the membrane." He also used plastic colored bird leg bands during this same study, which did not seem to cause damage to the wing, but the colors faded quickly and the numbers tended to wear off in time.

Alternatives to bat bands were experimented with during the BBP—most notably punchmarking (Bonaccorso and Smythe, 1972; Kleiman and Davis, 1974; O'Shea, 1975; Bonaccorso and others, 1976). Bonaccorso and others (1976) later found that punchmarks only remain legible for about 5 months. In the case of Kleiman and Davis (1974) and O'Shea (1975), punchmarks were also not useful except for short-term studies because the mark was illegible as soon as 6 weeks after application.

(2) Disturbance

Bat-banding activities during the BBP were linked to significant declines in bat populations because of disturbance during critical periods such as hibernation (Mohr, 1972; Tuttle, 1979; Barclay and Bell, 1988). Winter banding of hibernating bats was implicated as one of the major causes of population declines in species that hibernate (for example, Jones, 1976). One of the main motivations for the resulting banding moratorium of 1973 was anecdotal information on declines in 22 bat species. One hundred bat researchers were contacted in 1971; of theses, 73 responded and most respondents identified bat-banding activities as a major source of disturbance to bats, especially at roosts, and they recommended the restriction of the BBP in order to ease the disturbance of bat colonies (C. Jones, unpub. data, 1971). The indirect negative effects of handling and observer influence associated with bat banding activities was thought to be of greater magnitude than direct effects of injuries from bands.

Mohr (1972) summarized a few of the problems of human disturbance to bat populations. He described multiple scientific parties from a single university that had made at least 40 trips into a major bat cave in just one year. Reidinger (1972) noted that the most encounters between biologists and bats occurred in the major bat caves in June and July in Arizona when most bat species were pregnant or rearing young. Gunier (1971) reported on stress-induced abortion in gray myotis while banding at a maternity colony in Missouri. About a dozen bats spontaneously aborted fetuses while being handled and disturbed due to banding activities, which caused Gunier to recommend leaving maternity colonies undisturbed from early May through June. Cockrum (1969) also reported that pregnant Brazilian free-tailed bats would abort their young soon after capture.

S.R. Humphrey published several papers documenting the effects of bat-banding activities on bat colonies. He banded 88 Townsend's big-eared bats at two nursery roosts in western Oklahoma. The bats from one roost moved to a less suitable roosting area by the next month, and bats simply disappeared from the other roost and were never found again (Humphrey, 1969). Humphrey (1978) also reported on a biologist that banded all 250 Indiana bats at Bat Cave in Edmonson County, Ky., in 1971. By 1975, there were only 68 individuals in that same cave. In another roost also called Bat Cave, but in Carter County, Ky., Humphrey (1978) documented a decline of Indiana bats from 100,000 to 40,000; he attributed this largely to a long history of repetitious disturbance by biologists and park visitors. Cope and Mills (1970) studied the bat population in a hibernating colony of big brown bats in "Tunnel Cave" for five winters and reported that during this time, the disturbance by banding and the subsequent reading of bands caused unnatural movements in the cave. Bat population declines were not just linked directly to disturbance from banding activities. Other proposed causes for declines included contaminants, disturbance due to vandalism at roosts, recreational caving activities (spelunking), and natural calamities such as flooding of roosts.

Declines in bat populations due to banding activities were not unique to North America. R.E. Stebbings discontinued banding hibernating bats in eastern England caves due to noting substantial declines in the number of bats and negative effects of “ringing” (Stebbings, 1965, 1966a). He stated that the primary factor against conducting any bat study was the disturbance involved (Stebbings, 1966b). A long-term study of bat populations in the Netherlands showed a considerable decline in population from 1942 to 1957 (Sluiter and van Heerdt, 1957), but this trend reversed over the period 1958 to 1962 (Sluiter and van Heerdt 1964). The authors attributed this reversal to three factors: cessation of a banding program, cessation of quarrying in the vicinity of the roosting cave, and cessation of mushroom growing or other commercial use of the caves within the study area. Gaisler and Chytil (2002) reported that abundance of lesser horseshoe bats (*Rhinolophus hipposideros*) decreased from 1958 to 1963 in the Czech Republic and that this decline was probably due to the effects of mark-recapture work. At the 2d International Bat Research Conference held in Amsterdam, March 17–21, 1970, attendees listed in their detailed causes for bat population declines, “Banding or ringing of live bats causes damage and probably death to bats.”

(3) Problems with the BBP, File Management, and Recoveries

In addition to problems due to band injuries and disturbance to bat populations by banding activities, the BBP was also burdened by several additional issues that undermined its overall effectiveness as a clearinghouse for information on banded bats. These included the lack of an official permitting system for issuing bands, the lack of cooperation among bat banders, and frequent file management and reporting errors that led to suspect banding and recovery information.

Lack of Official Permitting System

The BBP was inconsistent in how they determined the qualifications and eligibility of requestors to band bats. Bat bands were often sent to people with no prior bat experience or bat “hobbyists.” Davis (1962a) noted that all too often a person obtained bands simply because of a passing curiosity. In the correspondence section of *Bat Research News*, 1962, R.H. Manville discussed an unofficial policy about issuing bat bands by the BBP. He stated that in general, bands should only be issued to cooperating scientists whose special projects required the use of banded animals. It was preferred that individuals with little experience or transitory interest were to work under the guidance of a recognized cooperator. After a period of “apprenticeship,” they could be issued bands in their own name. The problem of how to establish a policy for determining qualifications to band bats was discussed by many bat banders at meetings and in the correspondence files in the BBP. However, it was not until 1971 that a specific recommendation was made concerning this issue. In a memorandum dated June 2, 1971, from Clyde Jones, Chief of the Mammal Section, stated the following:

> “Bat banding should be controlled by permits issued only to qualified persons capable of handling bats. Minimal requirements for a permit should include a letter of intent, with a brief outline of the proposed banding project, and two recommendations from scientists or other banders with regard to the qualifications of the applicant. In addition, the permit should require that banders submit all banding data and a brief report to the central clearing agency at least annually.”

However, this recommendation was never established as an official policy due to the moratorium on bat banding put into motion a year later. An additional concern when allowing bat "hobbyists" to band bats and when using citizen volunteers from public recoveries of banded bats was the risk of rabies. Rabies was (and is) an important public health concern in the United States, and the most human rabies cases during the past half century were attributed to rabies virus variants associated with insectivorous bats (Messenger and others, 2002). Individuals who worked with bats were also at greater risk of rabies exposure than the general public. Currently (2008), the recommendations by various bat conservation organizations and the Centers for Disease Control and Prevention are that bat researchers should have the pre-exposure rabies vaccination and maintain an adequate titer to protect against the rabies virus. It is doubtful that many bat "hobbyists" banding bats during the BBP were aware of the risk of rabies. The first reported case of human rabies attributed to exposure from a bat was in 1951 (*http://www.batcon.org/pdfs/rabieschart.pdf*).

Lack of Cooperation among Bat Banders

There was a lack of cooperation among bat banders, which compromised recovery information. Cope and Hendricks (1970) stated that other researchers had removed both banded and unbanded bats from buildings in Indiana for physiological experiments unbeknownst to the authors, thereby confounding the results of their population studies. The authors made a plea for better cooperation among researchers. Manville (1962) found it discouraging when he learned that "a bat one has banded nearly 20 years before has been collected for studies in anatomy, physiology or virology." He further stated these studies, while important, did not depend on banded bats and asked that collectors refrain from taking banded specimens. Hitchcock had several of his big brown bats taken and skinned for museum specimens; one was much older than any recorded in the literature at that time (BBP files). In a memorandum to the BBP dated January 14, 1971, an active bat bander (name withheld) complained about the negligence of some banders to report recoveries shortly after they were found. He knew of another bat bander who had recaptured bats at his research colonies but had yet to report them to the BBP. He suggested that all banding records should be submitted by December 31 of the year of banding or the BBP should deny banding privileges to individuals failing to submit their records. William H. Elder also complained about the "laxness of bat banders in sending into the banding office information on recoveries they find in the field" (memorandum dated August 7, 1970). He also strongly recommended that the BBP "place all banding permits on an annual basis subject to renewal only when the previous year's banding returns and recovery data have been filed in Washington."

Problems with File Management and Reporting Recoveries

The BBP was plagued with problems related to file management and reporting errors resulting in incomplete files and invalid recoveries. Incomplete files were mostly a result of a lack of correspondence between banders and the BBP. Banders would often forget to return banding cards to the BBP. While conducting fieldwork, Davis (1962a) found half a dozen bats banded by others in New York and Connecticut. After reporting these numbers to the BBP, he was informed that the bands had been issued to two different banders 5 to 10 years previously and that these banders had never reported the data on these bands to the office (that is, they had never sent the index cards back to the office). Banders would also not fill out the index cards completely. Many cards did not include the State, sex or species identification of banded bats.

There was evidence that bands were often issued to one person, then handed down to someone else, and no information on this transaction was sent to the BBP. An illustration of this “grandfathering” of bands occurred in a banding study near Bend, Oregon. This study took place in the mid-1960s in Oregon Lava Tubes, and the three main banders were Larry Langley, Jim Anderson, and George Long. However, the bands themselves were originally issued to the Oregon State Board of Health under Dr. Monroe A. Holmes, D.V.M. I was only able to find two cards in the BBP files associated with this study. In this case, bands were issued to one person, passed on to someone else who then did not fill out the band information cards (reports) nor send the banding reports back to the BBP. In an unpublished summary dated March 16, 1972, written by Jim Anderson from the Bend Area Bat Study in the files, he reported banding a total of 190 bats: 159 Townsend’s big-eared bats, 16 little brown bats, 14 pallid bats, and one big brown bat. There were 24 band “returns” and no recoveries reported (all returns were for Townsend’s big-eared bats through 1971). During this study, they used anodized “bird-type” bands, not lipped bands. So in addition to not reporting banding of bats to the BBP, they were also applying harmful, straight-edged bird bands to the bats despite the ongoing experimentation with lipped bat bands and the evidence that these types of bands were better for bats. Harmful, straight-edged bird bands originally issued early in the BBP were therefore still being applied to bats into the late 1960s.

I found two more examples of the incompleteness of the BBP files. Conrad (1964) stated that the “author started to band bats in the Virginias in 1960,” but I found no records of this bander in the BBP files. This may be another example of bands issued to one bander and passed on to another bander with no record or trail to follow. H. Trapido was a bander in the early days of the BBP, and I found evidence that he did not record and send information about when, where, and what species he banded to the BBP (of six groups of bands issued with corresponding reporting cards, there were no records in the files of those bands having been applied to bats). For example, of 1,000 bands issued to Trapido in the series 140-58001 to 140-59000, I could only find banding reports completed by him for 27 little brown bats that were banded and later released over the Pacific Ocean, presumably for a homing experiment. However, several hundred bands in this same band series were later found on bats by C.E. Mohr at Aitkin Cave with no original record of banding by Trapido.

Errors often occurred in the filing process used by staff of the BBP. When a recovery or recapture was reported to the BBP, a green metal tag was supposed to be affixed to the index card containing the original banding information of the recovered bat. However, I found quite a few cards with recoveries handwritten or typed on the card, but with no corresponding green tags on the cards. I also found index cards with green tags attached to them, but with no recovery information written on the card. A recovery was sometimes recorded on the cards, but with no associated band number provided. Recoveries, recaptures, and resightings were all very different events, but the type of recovery was not always clearly written on many of the cards with green tags. In a memorandum dated January 14, 1971, to the BBP, an active bat bander (name withheld) complained about the incompetence of the BBP in returning proper recovery information. He cited one instance where the town was misspelled and the wrong directions were given for the site of the original banding. He then felt justifiably uncertain as to whether the band numbers were copied correctly onto the index cards by the BBP. He also complained that the BBP had not updated his current contact information to reflect his proper name and new address; as a result, important recovery information was being sent to an invalid address.

Another problem with reporting recoveries was inconsistent reporting by the public. Merlin Tuttle in the Correspondence section of *Bat Banding News* (Tuttle, 1961) stated:

> “I am rather discouraged about the prospects of anyone else ever reporting any of my banded bats. Recently a game warden caught one of my banded bats and said he threw it away because he didn’t know what to do with it. Two people have found my banded gray

bats (*Myotis grisescens*) in rather unusual places and taken them to the University. None of these people had any idea what should be done with the bands."

The validity of recoveries due to reporting errors was questioned throughout the BBP. Davis (1962b) questioned the validity of recoveries and went so far as to point out that there were so many mistakes, he had serious doubts about most recoveries. According to Davis (1962b), there were three places a mistake could be made: (1) the bander of the bat and his or her record-keeping; (2) the finder (of the recovered bat) in getting the number correct; and (3) the BBP in pulling the card or keeping files updated and correct. He claimed that for every 100 banded bats recaptured, he and his coworkers often made mistakes in recording the information on at least 2–3 bands, which could lead to erroneous information being associated with any subsequent recovery. He postulated two reasons for these mistakes made by banders: (1) handling too many bats in a short period of time,and (2) difficulty in reading the numbers on the bands because the stamping job was sloppy. The flat-topped number nine on some bat bands easily could be mistaken for a five. Number of recoveries reported was also suspect because the public would turn in banding information only to the banders who would then not necessarily report this information back to the BBP. Analyses of band recovery data based on public recoveries have many problems (Tuttle and Stevenson, 1977). These include inconsistency in reporting, inexact location information reported, small proportion recovered (that is, 71 recoveries of banded gray myotis were made by the public compared to 19,691 recoveries/recaptures made by authors during the same time period).

There was evidence in the BBP files that duplicate band numbers were issued (Greenhall and Paradiso, 1968; memorandum dated October 31, 2000, by S.C. Peurach). During her pilot data-entry study, Peurach found that many of the oldest cards for H.B. Hitchcock had sets of cards with the same band number, but with completely different information. Of the 3,500 records entered of Hitchcock's banding data, more than 466 of these included duplicate band numbers. Therefore, at least 13 percent of these records were duplicated, and if bats were recovered from this series of band numbers, it would be almost impossible to track down the correct information. Greenhall and Paradiso (1968) also stated this was a problem early on during the BBP. Apparently, duplicate band numbers were issued to both bird banders and bat banders simultaneously. This problem was solved in 1937 when the Bird-Banding Office began issuing unique bands to bat banders.

Extracting and summarizing information available in the BBP files was a time-consuming task and could cause errors in reporting and file management. The records for banded and recovered bats were kept on cards filed and sorted completely by hand. Computer and database management technology simply did not exist during most of the BBP. This meant that summarizing recoveries and searching for information on banded bats always required a tedious amount of work due to the large numbers of index cards and the lack of computerization of the files. Toward the end of the BBP, many discussions occurred about modernizing the files, and this often included the suggestion to enter all of the cards into a computer program. Mohr (1972) suggested computerizing data to make their use available to research scientists. In the memorandum dated June 2, 1971, a specific recommendation was made to the Chief of the Bird and Mammal Laboratories:

> "Plans should be made for future computerization of the bat-banding records. This should include the development of a standard form more suitable for recording as much field data as possible for each bat banded. Methods of input, storage, and retrieval of data should be established in accordance with either the application of flexowriter capabilities to facilitate data handling and input into a computer now in use in the Mammal Section or the established program of data processing utilized by the Bird Banding Office."

Recovery and recapture rates were low through the entire BBP. For the large numbers of bats banded from 1932 to 1972, numbers of recaptures and recoveries were not substantial enough to allow for the precise estimation of life-history parameters of interest such as survival or population sizes. For most mark-recapture studies to be successful in estimating population parameters precisely, the number of recoveries or recaptures needs to be large (Williams and others, 2002). Publications about the BBP and instructions for what to do if a banded bat was found were few and far between and were usually published in scientific journals or specific bat-related journals, not easily accessible to the general public (E.L. Davis, 1968). One way to have increased the number of incidental recoveries made by the public would have been to increase the awareness of the public to bats and the ongoing national BBP. For example, I found a quote in *Bat Research News* in 1971 (Volume 12, issue No.1) complaining that "there have been few band returns lately of bats banded by John Pawluk and Thomas Clancy in northern New York in 1963-1964; I attribute this to the current lack of public information about bats and bat banding in that area, as returns were numerous when the newspapers in that area carried stories on bat work." E.L. Davis summarized bat bands issued from 1965 to 1970 (566,600 bands were issued) in a memorandum dated July 23, 1970, to Clyde Jones. He included in this memorandum a list of banders and the number of bands issued to them. He further estimated the number of recoveries as being 2,500 per year, a recovery rate that strikes me as being too high after my review of the banding literature and examination of the information in the BBP files.

Case Studies

The following four specific case studies illustrate a few of the problems with USFWS bat bands and with the BBP files described above (for example, low recovery rates, incomplete files, band injuries, and indiscriminate banding).

(1) H.D. Walley Band Records

H.D. Walley with the Department of Biology, Northern Illinois University, was an active bander with the BBP in the 1960s. Most of his banding took place at the Blackball Mine in LaSalle County, Illinois. Blackball Mine is located in the Pecumsaugan Creek–Blackball Mines Nature Preserve, which was established in 1984. This preserve is in northern Illinois near North Utica and is currently owned by the Illinois Department of Natural Resources. The mine is one of the largest bat hibernacula in Illinois (*http://dnr.state.il.us/INPC/Directory/Sitefiles/Area3/PECLS.htm*). Five species of bats are known to use the mines; including the federally endangered Indiana bat (U.S. Fish and Wildlife Service, 1999). This case study illustrates low recovery rates, incompleteness of the BBP files, and disturbance to bats from banding activities.

According to Walley's publication in 1970, more than 12,000 bats were banded from 1961 to 1968 at Blackball mine, of which 7,873 were little brown bats (Walley, 1970). The main purpose for this banding was to look at seasonal movement patterns from summer recoveries of little brown bats banded in winter at the mine. He documented low recovery rates: only 38 of the 7,873 little brown bats were recovered in the summer, but these recoveries showed that dispersal of the bats closely correlated with the Illinois River watershed. All recoveries were from reports submitted by the public to the BBP. Walley (1970) also reported a recovery of an Indiana bat banded at Blackball Mine that was taken 3 years later in Missouri, which showed a greater dispersal distance for this species than was previously hypothesized. He also reported on a longevity record for an eastern pipistrelle of 14.8 years (Walley and Jarvis, 1971a, 1971b); a previous longevity record of 11.2 years was reported for this species (Paradiso and Greenhall, 1967).

While examining the BBP files in 1996, I investigated H.D. Walley's banding records and summarized his information to compare it with what he published in the early 1970s (table 3). Walley was issued 16,000 USFWS bat bands by the BBP from 1960 through 1972, which he applied to six species of bats all at Blackball Mine. For the series 29-126001 to 29-127000 (1,000 issued on November 9, 1960), I found only one report for one individual of an unknown species banded. For the series 65-05001 to 65-06000 (1,000 issued on November 9, 1960), there were 966 band reports on record. Three species were banded (little brown bats, northern long-eared myotis, and eastern pipistrelles), but there was no indication of how many bands were applied to which species. Five recoveries exist on file for little brown bats. For bands issued from 1961 through 1968, 8,324 little brown bats were banded with 125 recoveries on file, 317 Indiana bats were banded with only one recovery, 742 big brown bats with 11 recoveries on file, 5 eastern red bats with no recoveries, 179 northern long-eared myotis with no recoveries; and finally, 138 eastern pipistrelles were banded with no recoveries on file. Hence, there were discrepancies between Walley's banding information in his 1970 publication (Walley, 1970) and what was on file at the BBP office. Additionally, band-recovery information from the longevity record of the eastern pipistrelle from Walley and Jarvis (1971a; 1971b) did not exist in the BBP files.

In a memorandum from H.D. Walley to Barbara Harvey of the BBP dated April 12 1973, Walley brought up several issues related to banding and the Blackball Mine. He wrote that vandalism was becoming an increasing threat and suggested closing the entrances to the mine "with grilles through which bats, but not humans could pass." He also stated he felt that banding should be discontinued during the winter months. About band injuries, he wrote he had "observed little band injury in the Blackball Mine populations (approximately two out of every 100 banded showing chewing or overgrowth)." He further wrote that he felt "certain that awakening bats during the hibernation period causes considerable weight loss and mortality." Mammalogy classes from several universities apparently visited Blackball Mine each year and would awaken the bats for various measurements, collect bats for study skins, and sometimes remove 50–100 bats to take back to the universities for further studies. In conclusion of this memorandum, he suggested that the Blackball Mine should be given full protection, which later occurred in 1984.

(2) R.F. Myers Band Records

The BBP issued R.F. Myers 64,294 USFWS bands from March 1953 until February 1970. He mainly banded three species of *Myotis* (little brown myotis, Indiana bats, and gray myotis) roosting in multiple caves in the Ozark region of Illinois, Missouri, and Pennsylvania from 1954 to 1962 (Myers, 1964a) (Appendix 3). From the BBP files, I summarized his banding efforts at three different locations: (1) three caves in Camden County, Missouri; (2) Aitkin Cave in Mifflin County, Pennsylvania; and (3) Inca Cave, now Great Spirit Cave, in Pulaski County, Missouri. I summarized these three general locations to illustrate low recovery and recapture rates for banded individuals. The banding R.F. Myers conducted at these locations was never published, although he published information on *Lasiurus* bats from Missouri caves, one of which was Inca Cave (Myers, 1960). He also reported on interesting recaptures of two gray myotis in Kansas that he had banded in Missouri (Myers, 1964b). This case study illustrates the pervasive problem of very low recovery rates during the BBP.

Of the 1,467 gray myotis he banded in 1959 at three caves in Camden County, Missouri, there were reports of only two recaptured bats, one of which was a recovery and one a recapture. This was only a 0.004-percent recovery rate. Aitkin Cave is an important hibernaculum for multiple species of bats in Pennsylvania. It was gated in 1987 to protect the hibernating populations of

Table 3. Number of U.S. Fish and Wildlife Service (USFWS) bat bands issued, date bands were issued, species banded, reports of bands applied to bats, and reported recoveries for H.D. Walley's set of banding records in the Bat Banding Program files, U.S. Geological Survey, Patuxent Wildlife Research Center, Biological Survey Unit at the Smithsonian Institution, National Museum of Natural History, Washington, D.C. All bats were banded at the Blackball Mine in LaSalle County, Illinois. Recoveries include dead bats found by public.

Number of bands issued	Band numbers issued	Date bands were issued	Species code banded	Reports of bands applied (recoveries)
1,000	29-126001 to –127000	11/09/1960	Unknown	#29-12636 (0)
1,000	65-05001 to –06000	11/09/1960	MYLU MYSE PESU	966 (5 MYLU)
1,000	65-76001 to –77000	04/27/1961	MYLU	39 (1)
1,000	542-866001 to –867000	04/27/1961	MYLU	100 (0)
1,000	602-78001 to –79000	10/26/1961	EPFU MYLU MYSO	95 (3) 862 (12) 1 (0)
3,000	642-72001 to –75000	05/21/1963	EPFU LABO MYLU MYSE MYSO PESU	576 (7) 5 (0) 1,853 (43) 40 (0) 197 (1) 44 (0)
2,000	672-28001 to –31000	0 2/18/1964	EPFU MYLU MYSE PESU	41 (0) 57 (1) 41 (0) 47 (0)
3,000	7-12001 to –15000	1968	EPFU MYLU MYSE MYSO PESU	22 (0) 2,613 (34) 14 (0) 118 (0) 1 (0)
3,000	7-15001 to –18000	10/1968	EPFU MYLU MYSE MYSO PESU	8 (1) 2,800 (34) 84 (0) 1 (0) 46 (0)
5,000	7-61001 to –66000	No record of bands sent	MYLU PESU	1,299 (26) 2 (0)
2,000	A001-12001 to –14000	07/24/1972	None used	

eastern pipistrelles, small-footed bats, northern myotis, little brown bats, big brown bats, and Indiana bats. In 1993 it was dedicated as a Nature Conservancy Preserve (Richard O. Rowlands Preserve at Aitkin Cave: *http://www.nature.org/wherewework/northamerica/states/pennsylvania/preserves/art4333.html*). This cave has a long history of bat banding and research. Mohr conducted early banding efforts at Aitkin Cave in the early 1930s (Mohr, 1933b; 1936; 1942b; 1945). Trapido and Crowe (1946) also banded bats at this cave in the early 1940s. Hall and Brenner (1968) banded 1,269 individuals of five species of bats at this site during the BBP (1964–65) (Appendix 3). I found banding records in the BBP files at Aitkin Cave for the following two species: little brown myotis and eastern pipistrelle. Of 316 little brown myotis banded on March 15, 1953, only 16 (6.2 percent) were recaptured (7 were recoveries and 9 were recaptures). Of the three eastern pipistrelles banded, there were no reports of recoveries or recaptures.

Inca Cave, now called Great Spirit Cave, in Pulaski County, Missouri, is an important maternity colony for the endangered gray myotis and a hibernaculum for the endangered Indiana bat. Populations of both of these species populations have declined over many years across their range (Ellison and others, 2003). It was estimated as many as 250,000 gray myotis roosted at one time in Great Spirit Cave during the summer months (*http://chouteau.missouri.org/chouteaunews/2001-05/page5.html*). R.F. Myers banded up to eight different species at this cave during summer, fall and winter from 1955 to 1958. He banded 210 little brown bats, 2,267 Indiana bats, 303 gray myotis, 19 northern long-eared myotis, two big brown bats, 20 eastern pipistrelles, 10 eastern red bats, and one hoary bat (*Lasiurus cinereus*) for a total of 2,832 individuals. The largest recovery and recapture rate for any of the banding he did was for a group of 985 Indiana bats banded on March 10, 1957 (table 4). The total number of recaptures for this group was 126; 22 (0.2 percent) of those were recoveries and 104 (10.6 percent) were recaptures. Of 377 Indiana bats banded on February 18, 1955, 32 were recaptured: 14 (3.7 percent) recovered and 18 (4.8 percent) recaptured. Of the 347 individuals of eight different species banded on September 17, 1958, none were recaptured or recovered.

(3) W.H. Davis Band Records

W.H. Davis was an active bander with the BBP in the late 1950s and into the 1960s. He was also the editor and founder of *Bat Banding News/Bat Research News* from 1960 to 1970, during the first decade of its existence. He was issued 87,000 USFWS bat bands from 1959 to 1966, which he applied to multiple species of bats in Kentucky, New Mexico, New York, West Virginia, and Wisconsin. He investigated hibernation ecology and sex ratios (Davis and Hitchcock, 1964), homing behavior (Davis and Barbour, 1970a; Davis and Hardin, 1967), population dynamics (W.H. Davis, 1966b), migration and natural history (Davis and Hitchcock, 1965), and swarming behavior (Davis, 1964b). Bat Cave in Carter County, Kentucky, was one of the main locations W.H. Davis banded bats during multiple seasons from 1963 to 1974. Bat Cave is located in Carter Caves State Resort Park. Bat Cave was designated a nature preserve in 1981 for the protection of the endangered Indiana bat (*http://www.naturepreserves.ky.gov/stewardship/ batcave.htm*).

I summarized W.H. Davis' banding efforts at Bat Cave located in the BBP files to illustrate low recovery rates and low recaptures for this particular location (table 5). He banded six species of bats at Bat Cave: 2,579 little brown myotis, 13,414 Indiana bats, 1 northern myotis, 24 big brown bats, 27 eastern pipistrelles, and 37 eastern red bats, for a total of 16,082 individuals banded. Recovery rates were very low for every species ranging from 0 for many species of bats banded to 0.01 percent (15 recoveries for 1,601 little brown bats; table 5). Recapture rates were even lower with 0.003 percent for Indiana bats (8 recaptures of 2,456 banded) representing the highest recapture rate for all groups of bats banded.

Table 4. Number of U.S. Fish and Wildlife Service (USFWS) bat bands issued, date bands were issued, location of banding, dates bats were banded, species banded, reports of bands applied to bats, and total recaptured for R.F. Myers' set of banding records in the BBP files, U.S. Geological Survey, Patuxent Wildlife Research Center, Biological Survey Unit at the Smithsonian Institution, National Museum of Natural History, Washington, D.C. Summaries were made for three caves in Camden County, Missouri, Aitkin Cave, Mifflin County, Pennsylvania, and Inca Cave, now Great Spirit Cave, Pulaski County, Missouri. Total recaptured includes number recovered and number recaptured by bander.

Number of bands issued	Band numbers issued	Date bands were issued	Location	Date bats were banded	Species banded	Reports of bands applied (AM:AF)*	Total recaptured (recoveries: recaptures)
3,000	10-37001 to –40000	03/19/1959	3 caves, Camden County, Mo.	6/4/1959	MYGR	1,467	2 (1:1)
200	21-92201 to –92400	03/02/1953	Aitkin Cave, Mifflin County, Pa.	3/15/1953	MYLU PESU	195 (104:91) 1 (1:0)	10 (3:7) 0
300	21-92601 to –92900	03/09/1953	Aitkin Cave, Mifflin County, Pa.	3/15/1953	MYLU PESU	121 (73:48) 2 (1:1)	6 (4:2) 0
5,000	24-91001 to –96000	02/07/1955	Inca Cave, Pulaski County, Mo.	2/18/1955	MYLU MYSO PESU	101 (67:34) 377 (159:218) 12 (8:4)	4 (1:3) 32 (14:18) 0
5,000	25-70001 to –75000	11/16/1956	Inca Cave, Pulaski County, Mo.	3/10/1957	MYLU MYSO LABO	40 (25:15) 985 (478:507) 1 (0:1 juv)	4 (3:1) 126 (22:104) 0
5,000	25-75001 to –80000	04/08/1957	Inca Cave, Pulaski County, Mo.	12/22/1957 8/24/1957	MYSO LABO	385 (189:196) 8 (5:3 juv)	3 (3:0) 5 (5:0) recovered two months later
2,000	27-08001 to –10000	03/17/1958	Inca Cave, Pulaski County, Mo.	4/27/1958 7/17/1958 12/14/1958	MYGR MYSE MYSO	73 (55:18) 4 (4:0) 11 (5:6)	2 (2:0) 0 0
500	10-20001 to –20500	09/08/1958	Inca Cave, Pulaski County, Mo.	9/17/1958	MYGR MYLU MYSE MYSO PESU EPFU LABO LACI	230 (60:170) 69 (65:4)) 15 (14:1) 9 (7:2) 20 (11:9) 2 (1:1) 1 (1:0) 1 (0:1)	0 0 0 0 0 0 0 0
2,500	10-34001 to –36500	11/24/1958	Inca Cave, Pulaski County, Mo.	12/14/1958	MYSO	500 (260:240)	6 (5:1)

* AM is number of adult males and AF is number of adult females.

Table 5. Number of U.S. Fish and Wildlife Service (USFWS) bat bands issued, date bands were issued, dates bats were banded, species banded, reports of bands applied to bats, and total recaptured for W.H. Davis' set of banding records in the Bat Banding Program files, U.S. Geological Survey, Patuxent Wildlife Research Center, Biological Survey Unit at the Smithsonian Institution, National Museum of Natural History, Washington, D.C. Summaries are made for bats banded at Bat Cave in Carter County, Kentucky. Total recaptured is also included with number recovered (either by bander or public) and number recaptured (by bander).

Number of bands issued	Band numbers issued	Date bands were issued	Dates bats were banded	Species banded	Reports of bands applied (AM:AF)*	Total recaptured (recoveries: recaptures)
10,000	632-00001 to –100000	12/05/1962	Summer, 1963	MYLU	1,601 (1,178:423)	17 (15:2)
				MYSO	3,822 (2,994:828)	16 (11:5)
				PESU	1 (0:1)	0
10,000	632-45001 to –55000	03/11/1963	Summer, 1963 and 1965	MYLU	203 (150:53)	0
				MYSO	1,108 (1,064:44)	5 (1:4)
				EPFU	17 (1)	1 (1:0)
				PESU	15 (0)	0
				LABO	18 (0)	0
10,000	652-00001 to –10000	09/19/1963	Fall and Winter, 1963–1974	MYLU	662 (397:265)	9 (7:2)
				MYSO	3,828 (10)	10 (9:1)
				EPFU	6 (0)	0
				PESU	1 (0)	0
10,000**	652-18001 to –28000	10/13/1963	Winter, 1963 and 1964	MYSO	2,200 (1,200:1,000)	6 (4:2)
10,000***	652-75001 to –85000	11/07/1963	Multiple season, 1964–1965	MYLU	113 (38:75)	0
				MYSE	1 (1:0)	0
				MYSO	2,456 (1,314:1,142)	11 (3:8)
				EPFU	1 (1:0)	0
				PESU	10 (10:0)	0
				LABO	19 (14:5)	0

* AM is number of adult males and AF is number of adult females.

**Transferred 652-24002 to 25000 to M.J. Harvey in 1964 and transferred 652-23001to 24000 to D.J. Fassler in 1972.

***Transferred 652-75001 to 75500 to M.J. Harvey in 1964 and returned to banding office 652-77001 to 77100 on 08/24/1966.

W.H. Davis' banding files also illustrated the problem of "grandfathering" of bat bands. He transferred about 1,500 USFWS bat bands to M.J. Harvey in 1964 and another 1,000 to D.J. Fassler in 1972. In this case, the BBP was made aware of this transfer, but many times bat bands were transferred or handed down to other bat biologists without clearing or even notifying the BBP of the transfer (Peurach, 2004).

(4) Banding at Jewel Cave National Monument

The story of bat banding at Jewel Cave National Monument (U.S. Department of Interior, National Park Service) illustrates multiple problems with the BBP. Bats were banded at this location by people with no prior bat experience, illustrating the problems that can arise due to the lack of a permitting system to band bats. Additionally, there were both injuries to Townsend's big-eared bats from the application of bands and low recovery/recapture rates. J.T. Stokes first recommended banding bats at Jewel Cave in an unpublished memorandum from 1959 entitled "Behavior and habits of bats as observed in Jewel Cave National Monument." Because of this memorandum, the superintendent of the park requested 4,000 No. 0 (*sic* No. 1?) bat bands on December 2, 1959, from the BBP, and the park was sent 3,000 of these bands on December 9, 1959. A park naturalist named J.A. Tyers was the intended bander, but he had no prior bat experience. By December 1961, 1,969 Townsend's big-eared bats were banded during the winters of 1959, 1960, and 1961. In a memorandum dated June 20, 1962, park naturalist J.A. Tyers first noted problems with the bands. He stated the park has been using No. 1 size bird leg bands and that a "large percentage of these banded bats have developed an abnormal growth where the band was affixed to the wing." In a later memorandum from the superintendent, this percentage was given as 40–50 percent. He further stated, "since our bands for this program are obtained from the Fish and Wildlife Service's Mammal Distribution section through the bird banding office, it seems this would be the office to contact in an attempt to instigate a change in the type of band supplied." In the correspondence section of the 1963 *Bat Banding News*, the superintendent of Jewel Cave was quoted:

> "This past year a survey was made on November 23 (1962) and it was discovered that of 324 (bats) observed, 89 had no bands, 83 were banded and showed no injury, and 152 exhibited varying degrees of injury from bands imbedded in the flesh. With an incidence of 65 percent showing injury, it was felt we were doing more harm than good. We have therefore temporarily discontinued banding until a more suitable band is available than the No. 1 band."

The BBP then suggested to Jewel Cave that they try using No. 2 size bands on Townsend's big-eared bats, but they warned that misapplication of this larger band could also cause injuries to the bats. If the No. 2 size band was pressed closed with too much force, this could cause as much injury as the smaller No. 1 band. Conversely, by applying the No. 2 bands too loosely, irritation could also occur because of the band slipping too far up and down the length of the wing bone.

Only one foreign recovery for bats banded during 1959–61 was reported in the eastern part of the Black Hills (memorandum dated September 1, 1960). Jewel Cave requested 2,000 No. 2 size bands on September 17, 1963, and in December 1963, 191 bats were banded with this type of band. There were no records of further banding with this size band after the winter of 1963. A female Townsend's big-eared bat banded in Jewel Cave on December 24, 1963, was recovered in June of the following year on the western edge of the Black Hills.

Part 2. Discussion of Mark-Recapture Techniques and Utility of the Existing Bat Banding Program Data

In this part I review basic mark-recapture techniques used to estimate two important biological parameters: population size and survival. I will then discuss the utility of the existing BBP files to answer questions about these two parameters. Important historical information on bat populations could be buried in the BBP files, but to make this information available for analyses, a huge effort would be required to enter and computerize the files. The numerous problems with the BBP and its files detailed in Part 1 would have to be addressed seriously before making any concerted effort to computerize the BBP files and conduct *post hoc* analyses of the data for population size and survival estimation.

In reviewing mark-recapture techniques, I will briefly discuss four main methods available for the analysis of data on marked animals (Lincoln-Petersen method, *K*-sample closed population models, band recovery models, and open population models). I will also discuss model selection procedures and study design issues related to mark-recapture studies. For all of the models I describe, the resulting parameters are estimated with the use of maximum likelihood methods. Maximum likelihood methods produce estimates with good properties under a wide range of conditions (Amstrup and others, 2005). In statistical terminology, the method of maximum likelihood provides estimates that are asymptotically unbiased, normally distributed, and of minimum variance (Lebreton and others, 1992). There are two steps in a very basic description of maximum likelihood methods: (1) there is the construction of a model that states the probability of observing the data as a function of the unknown parameters that are of interest; and (2) the estimates of the unknown parameters are chosen to be those values that make the likelihood function as large as possible (that is, the values that maximize the likelihood) (Amstrup and others, 2005). There is a huge body of primary literature sources and excellent comprehensive books available on mark-recapture theory and analysis methods. For more detailed and complete reviews of mark-recapture techniques, see Lebreton and others (1992), Williams and others (2002), and Amstrup and others (2005).

In this and the following parts of this report, I will frequently cite Program MARK. Program MARK is the most comprehensive software application currently available for the analysis of data from marked individuals (White and Burnham, 1999; White, 2008). There are currently more than 65 data types programmed in this software for the estimation of population parameters from mark-recapture data (White, 2008). Although the learning curve is steep for becoming proficient in MARK, it offers far more flexibility and power in statistical modeling and hypothesis testing than other widely available programs. It is freeware and available online at *http://welcome.warnercnr.colostate.edu/~gwhite/mark/mark.htm* and the mirror site at *http://www.phidot.org/software/mark/*. A very thorough “Gentle Introduction” to MARK is also available online at *http://www.phidot.org/software/mark/docs/book/*.

Mark-Recapture Techniques

Models to Estimate Population Size

An important parameter in population biology is abundance or population size, which simply refers to the number of individual organisms in a population at a particular time. Abundance is a variable of key interest in studies of population dynamics; therefore, it is important to estimate this parameter as precisely as possible. Population size can be estimated based on observations of animals without capturing them, but many wildlife species are cryptic and not easily observed. Capturing and marking individuals for later identification can be used to estimate population size for animals that are more difficult to observe (for example, bats).

The two basic models I will review that are most relevant to a discussion of the value of the BBP files are the simple two-sample Lincoln-Petersen estimator and the models for sampling situations with greater than two occasions (also called *K*-sample mark-recapture models; Williams and others, 2002). The major assumption underlying both of these models is “closure.” The population is assumed to be closed to additions (by birth and immigration) and losses (by death and emigration) during the course of the study (Williams and others, 2002). Another assumption common to both of these models is that marks are neither lost nor overlooked. The final assumption for both models concerns the capture probabilities. In the Lincoln-Petersen case, all animals are assumed to be equally likely to be captured in each of the two samples. In the *K*-sample mark-recapture framework, capture probabilities are appropriately modeled incorporating capture heterogeneity among individuals, behavioral responses to capture, and (or) temporal variation.

The Lincoln-Petersen estimator is appropriate to use when there are just two sampling occasions and the interval between the occasions is relatively short. The Lincoln-Petersen estimator can be derived in several ways, but the simplest is to note that the proportion of marked animals in a population after the first sampling occasion is n_1/N where n_1 is the number of animals captured and marked in the first occasion and N is the population size (Williams and others, 2002). If all animals are equally catchable, this proportion approximates the proportion of marked animals in the second sample so that $n_1/N = m_2/n_2$ where m_2 is the number of animals captured in both occasions and n_2 is the number of animals captured in the second occasion. The estimate of population size is therefore the product of the number of animals captured in the first and second period divided by the number of marked animals.

The *K*-sample mark-recapture approach is appropriate to use when there are more than two sampling occasions (for example, capturing and marking bats at a roost for five continuous evening emergences). At each sampling occasion, previously uncaptured animals are marked and individual identification marks of previously marked animals are recorded. The resulting capture history matrix is a series of vectors of 1s and 0s indicating the sequence of captures for each individual during the study. This matrix can then be summarized in statistics that denote the number of animals exhibiting each possible capture history. The next step is to model the capture probabilities by incorporating heterogeneity among individuals, behavioral responses, and temporal variation. For decades Program CAPTURE was the most frequently used software to estimate population sizes using closed population models (Otis and others, 1978). Currently, all of the likelihood-based models from CAPTURE can be built in Program MARK (White, 2008). The resulting parameter estimates provided are population size and, depending on which model is selected that best fits the data, a variety of capture and recapture probability estimates.

Models to Estimate Survival

Mark-recapture theory and the general analysis of capture data have both advanced substantially in the past 25 years. During the mid-1980s, the primary focus of the analysis of mark-recapture data started to change from the estimation of population size to the estimation of survival (Lebreton and others, 1992). While the abundance of animals is still a variable of interest, survival and recruitment are the underlying reasons why population size changes over time (Franklin and others, 2002). Survival estimators are also substantially more robust to the failure of basic assumptions of mark-recapture theory than are estimators of population size. The two basic models used to estimate survival that are the most relevant to an evaluation of the BBP files are band-recovery models and the basic Cormack-Jolly-Seber (CJS) model for open populations. Band-recovery models were developed in the mid-1960s to early 1980s and the focus was primarily with bird-banding data (Brownie and others, 1985). The original theory was also developed to estimate survival of exploited species of birds such as waterfowl (for example, pintails, mallards) where large numbers of these birds were banded and records were kept by the BBL on the number of bands reported from dead birds for consecutive years after initial banding. CJS models were developed over several decades based on the foundational work of Cormack (1964), Jolly (1965), and Seber (1965).

Band recovery (or tag recovery) models involve procedures for estimating survival, recovery, and harvest rates based on recoveries of tags. Recoveries are from animals that have been marked or tagged, released, and subsequently either found dead and reported or have been harvested, retrieved, and reported by hunters or anglers (Williams and others, 2002). Bats are not a harvested (or hunted) species, so I will focus this summary on the analysis of band recoveries from nonharvested species, which is an extension of the theory developed for hunted species. In this case, the parameters of interest are survival and a "reporting rate." The reporting rate is the probability that the marked, dead animal is found and its band is reported by the finder. Reporting rates are conditional probabilities (conditional on death), and reports on recovered animals can occur throughout the interval between banding occasions. Key assumptions of band recovery models are that the sample is representative of the population under investigation, there is no band or tag loss, the age and sex of the sampled individuals are correctly determined, the year of band recovery is correctly noted, and survival rates are not affected by the banding or tagging technique.

The basic CJS open population model allows for losses and gains to the sampled population. As an open population, changes can occur during the course of the study because of any combination of birth, deaths, immigration, or emigration (Amstrup and others, 2005). The CJS model is based solely on recaptures of marked individuals and provides estimates of survival, ϕ, and capture probability, p. The parameter for survival, ϕ, combines the probability the animal is alive and the probability it remains in the study area and is available for capture. In mark-recapture literature, ϕ is referred to as "apparent survival" or "local survival" (Williams and others, 2002). The framework for these studies includes $K > 1$ sampling occasions where animals are captured and on each occasion, new (unmarked) animals are given unique marks and then are released back into the studied population. The resulting capture history is a matrix of 1s and 0s for each sampling occasion similar to the capture history for K-sample closed population models described previously. Apparent survival and capture probabilities can be modeled with parameters of biological importance such as age, sex, environmental conditions, and individual covariates (for example, body mass, number of ectoparasites) in Program MARK. The assumptions for the CJS model are the following: "(1) every marked animal present in the population at sampling period i has the same probability p_i of being recaptured or resighted; (2) every marked animal present in the population immediately following the sampling in period i has the same probability ϕ_i of survival until sampling period $i + 1$; 3) marks are neither lost nor overlooked, and are recorded correctly; (4) sampling periods are instantaneous (or in reality, very short periods) and recaptured animals are released immediately; (5) all emigration from the sampled area is permanent; and (6) the fate of each animal with respect to capture and survival probability is independent of the fate of any other animal" (Williams and others, 2002:422).

Model Selection Procedures

The basic analytic process for all of the above mark-recapture models involves developing probability models for the biological processes that best describe the capture histories collected in the field from marked individuals. The process involves finding the "best approximating model" from a set of *a priori* candidate models to estimate important parameters and make inferences about populations (Burnham and Anderson, 2002). Finding the best model to fit the capture data requires a lot of thought about the biology of the species and what environmental factors may be influencing their population dynamics. Once a set of models is defined, their rankings can be determined using the information-theoretic approach and Akaike's information criterion (AIC) (Burnham and Anderson, 2002). AIC provides a simple, effective, and objective means for selecting a best approximating model from a set of candidate models. In cases where capture data are sparse, a small-sample version of AIC is available (AIC_c). Many times the sampling variance exceeds the model-based variance due to a lack of independence in individual responses (to capture). This is called "overdispersion," and quasi-likelihood methods should be used in these cases (QAIC and $QAIC_c$). Usually a combination of statistics is used to assess the validity and fit of the different models such as AIC, ΔAIC, AIC weights and their small-sample, quasi-likelihood versions, all of which are provided in Program MARK.

Study Design Issues

Study design has an important function in any mark-recapture endeavor. As with any estimation method, the results from a marking study are only as good as the data used in the procedure (Williams and others, 2002). It is therefore vital that any mark-recapture study be conducted in such a way that the assumptions for the models will be reasonably met to ensure the estimates are unbiased and apply to the target population. The main study design issue common to all of the models described previously is that the banded population should be as representative of the population at large as possible. This means that the act of banding should not in any way negatively affect the animals or cause them to act differently than unbanded animals. It is also important to select a marking or banding method that minimizes "tag loss." If age and sex differences are important to survival and recovery or recapture probabilities, these vital statistics should be accurately determined. Time of year when sampling occurs is also an important consideration because if capture and banding occur during significant movement, mortality, or recruitment events, unless this is accounted for in the models developed, parameter estimates will be biased. The duration of banding should be short relative to the interval over which the parameters will be estimated (for example, if banding periods extend too long, mortality or movement will occur, which leads to heterogeneity in survival rates wherein animals banded at the beginning of the marking period are at risk of dying or moving longer than animals banded at the end). Duration of the banding study is an important consideration: the longer the better. For survival estimation, the standard suggestion is that at least 3 years and preferably 5 or more years are required to obtain an adequate sample size of banded individuals and to investigate temporal variation in survival and other parameters. Sites where banding occurs should ideally be randomly distributed across the landscape; however, locations generally are chosen on the basis of logistic considerations (for example, for bats, banding is mostly conducted where they aggregate or roost, such as in caves or buildings). For open population models, such as CJS, it is important to consider the assumption that animals are not permanently emigrating from the study site. Finally, a concerted effort should be made to ensure large capture probabilities. Capture, recapture, and recovery parameters are often called "nuisance" parameters, but as these probabilities increase, the more vital parameters such as survival and population size can be more precisely estimated (Williams and others, 2002).

Utility of Existing Bat Banding Program Files

Historical data are valuable to science by providing a necessary baseline of information for making comparisons to current-day situations. The information located in the BBP files represents a considerable amount of effort in time, money, and people-hours. Therefore, a critical upfront evaluation of the information located in the files is important before considering the huge effort needed to make the data available for retrospective analyses for population size and survival estimates. A fundamental concern to note for any retrospective population analysis is that the estimates derived are historical, after the fact, and may not be applicable to current day research needs or management issues. It can be difficult to conduct any mark-recapture study on any group of animals properly without a considerable amount of *a priori* planning in study design. Even if the information in the BBP files could be used to estimate population size or survival accurately for multiple species of bats, there are two major concerns that need to be addressed: (1) is it worth the effort and funding to know what these estimates were decades ago, and (2) would we learn much more than what is already known from the scientific literature?

It might be possible to estimate population sizes of bats using select subsets of data from the BBP files. However, these estimates would be for specific locations and points in time and not necessarily comparable over the complete range of the species and (or) over time. A main reason for estimating population sizes is to see how they change over time. Population trends gleaned from the BBP files would only be over relatively short periods of time; very few long-term bat-banding studies exist in the BBP files (as mentioned in Part 1, only four published banding studies occurred for more than 20 years). However, these data might still be useful if someone wanted to repeat a study at a location for which historical data exist to quantify a change in abundance between two points in time. Of the population size-estimation techniques I described herein, the Lincoln-Petersen method was used in six of the banding studies published. There would be several problems in estimating population sizes and assessing trends after the fact, by using the Lincoln-Petersen method. The population estimates would be collected using questionable sampling schemes, and individual bats are not equally catchable, a major assumption of the Lincoln-Petersen method. Unequal catchability leads to biased population size estimates (Thompson and others, 1998). No population size estimates for bats during the BBP have been made using *K*-sample mark-recapture techniques where heterogeneity in capture probabilities could be modeled. It may be possible to find a few datasets within the BBP files where the *K*-sample framework could be applied to a few bat species, but this would again only provide historical point estimates not necessarily comparable to each other over time. The subsets of data in the BBP files would have to be chosen very carefully to ensure that the assumption of closure is met. Fundamentally, while population size is an interesting variable, it is more important to investigate the reasons why populations change in size over time (Franklin and others, 2002). Survival and recruitment are the main reasons why populations change over time, so investigating trends in these variables would be a more useful endeavor.

Post hoc analyses of the BBP files for survival estimation and trends in the probability of survival might be possible with a few select subsets of banding data. However, these subsets of data would have to be chosen very carefully to include studies with clearly defined and consistent methodologies, large numbers of recaptures, and at least 3 years' duration. In reviewing the BBP files and the literature on bat-banding data, I believe that most datasets that satisfy these requirements have already been analyzed and published. The analytical techniques used to estimate survival did not use current likelihood theory and model selection procedures, but the value of reanalyzing these data is questionable (based on the quality of the information in the BBP files). In Part 3 of this report, I provide a retrospective analysis from a select dataset in the BBP files using open CJS models to estimate survival probabilities. I considered this dataset for analysis because the card files appeared more complete than any other dataset and the number of recaptures was high.

Band recovery models could be used to analyze select information buried in the BBP files. I will illustrate the many potential problems associated with this process by comparing it to several *post hoc* analyses conducted on data from the North American Bird Banding Program (NABBP). The NABBP began as an official program in 1902 and has since served as the repository for bird banding data in North America. The Bird Banding Laboratory (BBL) currently administers the NABBP and is located at the U.S. Geological Survey, Patuxent Wildlife Research Center in Laurel, Maryland (*http://www.pwrc.usgs.gov/BBL/*; Haseltine and others, 2008). The BBP and how it was administered was modeled after this concurrent, but ongoing, program for tracking banded birds. However, the scope and scale of bird banding efforts vastly exceeds efforts during the BBP. The

BBL has records for an estimated 50–60 million banded birds (926 species) with many locations having continuous banding programs for 30–40 years (Franklin and others, 2002). It is estimated that 1.1 million birds are banded annually (*http://www.pwrc.usgs.gov/BBL/homepage/howmany.htm*). During the entire BBP (1932–72), it was estimated that about 1.5 million bats were banded (E.L. Davis, 1968).

Wotawa (1993) used band recovery models to examine long-term trends on survival probabilities by using a single 26-year dataset for mallard ducks (*Anas platyrynchos*). He found a long-term, negative linear trend in survival for both male and female mallards, but only because of the long-term nature of the dataset, the large numbers banded every year, and the high recovery rates. This trend would probably have been missed with a shorter data set (say 5–10 years) (Franklin and others, 2002). Franklin and others (2002) analyzed long-term trends and variation in survival probabilities for 129 bird species by using band-recovery models and data obtained on banding and recovery data from the BBL. They used a very strict set of criteria to select the datasets used in their analysis: there had to be more than 24 years of continuous banding of a species at one general banding site, there had to be a minimum of 50 birds banded each year with no gaps, and there had to be at least a total of 200 direct (that is, first year after banding) and 200 indirect recoveries. Only 16 species of the 926 species banded from the BBL met all of the criteria for selection of datasets. As with bats banded during the BBP, most species of birds banded during the NABBP were few in number and most had a very low ($f < 0.01$) annual recovery probability (Franklin and others, 2002). They concluded that current data collection by the BBL was inadequate for monitoring survival in most avian species in North America. Francis (1995) evaluated the bird "ringing" data for four species of birds with moderate numbers of recoveries. He noted that a main problem in the analysis and interpretation of data from band recovery of unharvested species was that recovery rates for many species (for example, passerine birds) were very low, resulting in sparse recovery data and estimates of poor reliability (Francis, 1995). He concluded that with current technologies and recovery rates, demographic studies for the vast majority of passerines in North America will need to rely primarily on data from live recaptures, not recoveries. In many cases the data for passerines were unusable for survival analysis, and far more reliable estimates of survival could be obtained with more focused mark-recapture studies (for example, CJS-based studies).

A few key assumptions and study design issues common to any mark-recapture model used to estimate population size and survival are that the sample is representative of the population under investigation, there is no band or tag loss, data are recorded correctly (that is, the age and sex of the sampled individuals are correctly determined and the year of band recovery or recapture is correctly noted), and survival rates are not affected by the banding technique. The BBP files are incomplete and not well organized, and recaptures and recoveries are suspect as detailed in Part 1, leading to violation of many of these assumptions and study design issues. There is evidence that band number information was frequently lost due to the soft alloy used by the manufacturer of the bands. Numerous errors occurred in recording data on the index cards by the banders and in the BBP filing process. Probably most importantly, many of the bands applied to bats caused injuries and sometimes direct mortality. Recoveries and recaptures were low and highly uneven among different bat species and geographic locations. Low recoveries and recaptures lead to imprecise estimates with high coefficients of variation. With all of these problems in mind, any estimates derived from retrospective population size or survival analysis of the BBP files would be biased, leading to questionable conclusions.

Part 3. Data-Management Case Study and Retrospective Survival Analysis of Townsend's Big-eared Bat (*Corynorhinus townsendii*) from Washington State

Introduction

With the limitations identified above in mind, my third objective for this report is to provide a case study in managing data and applying current mark-recapture theory to estimate survival using the information from a series of bat bands issued to C.M. Senger. Senger banded bats in Washington from the fall of 1964 until the winter of 1975 (Senger and others, 1972, 1974) with resightings noted until as late as winter 1980. He and his associates banded eight different bat species, but the majority of bands were applied to the Townsend's big-eared bat, a species of special concern for many States within its geographic range, including Washington (*http://wdfw.wa.gov/wlm/diversty/soc/soc.htm*), and a Federal Species of Concern (formerly Category II [C2]) (U.S. Fish and Wildlife Service, 1994; Pierson and others, 1999). In this part, I provide an example of data management of Senger's banding records and a retrospective analysis of survival. I use current mark-recapture theory and modeling capabilities that were not available when most bats were banded during the BBP.

I chose Senger's banding records for this case study for several reasons. First, in my initial assessment of the BBP files, the group of band reports submitted by Senger had the largest number of green metal tabs per card, all representing recaptures, of any other bander. Second, I was able to contact Senger and obtain his original electronic data of captures and recaptures by cave during the time when he was actively banding. This enabled me to compare his original records to the records on file with the BBP (C.M. Senger, oral commun., 1997). Additionally, the species he focused his banding effort on was Townsend's big-eared bat, a species of conservation concern. Finally, this effort would perhaps answer the following questions people have brought up since the moratorium in 1973 about the value of the BBP files: How good are the best of the records in the BBP files? Are the results obtained from a retrospective analysis strong enough to justify computerizing all of the remaining banding records for other species and locations? What quantitative and qualitative guidelines should be considered in deciding which BBP files should be entered into a database for the purpose of survival estimation?

The BBP issued 2,200 bat bands to Senger beginning in 1964. These bands were numbered 662-18001 to 662-18500, 672-33001 to 672-33200, 5-23501 to 5-24000, and 6-10001 to 6-11000. Banding mostly took place in the fall and winter of October 1964 through December 1975 in four counties in Washington: Klickitat, Skagit, Skamania, and Whatcom. Skagit and Whatcom Counties are located in the northwest part of the State, and Whatcom borders British Columbia, Canada. Klickitat and Skamania Counties are located in the southwest corner of the State, and both border Oregon. Banding of Townsend's big-eared bats occurred in all four counties, but the main focus of banding in the southwestern part of the State took place at two caves in Klickitat County (Jug Cave and Poachers Cave) and 12 different caves in the area around Mount St. Helens. In the northwestern part of the State, most banding of Townsend's big-eared bats occurred at Blanchard Mountain Cave in Skagit County, now called Senger's Talus Cave. In Whatcom County, a small group of Townsend's big-eared bats were banded at a location called Chuckanut Mountain. Senger's original objective for this banding, especially in the area around Mount St. Helens, was to "band a large number of animals which could be studied for a period of years, perhaps as many as 25" (Senger, 1969). The data he hoped to obtain from the study were: (1) movements of bats from cave to cave or from cave to feeding sites within the area; (2) movement from the Mount St. Helens area to other nearby or distant locations; (3) the extent to which bats return to the cave or site of original banding in subsequent years; (4) the survival of individuals, which would provide an indication of the life span; and (5) the proportion of unbanded bats in the population each year as an indication of reproductive success.

There were three main goals to my analysis of Senger's data: (1) to develop a database management system for the bat-banding records and use Senger's files as pilot data to enter, query, and summarize; (2) to analyze and model survival and capture probabilities of hibernating Townsend's big-eared bats at three main locations in Washington using Cormack-Jolly-Seber (CJS) open models and the modeling capabilities of Program MARK; and (3) to discuss the value, precision, and violation of assumptions surrounding the resulting survival estimates in relation to the BBP files.

Methods

Database Management

I designed a relational database to collect and store data from the BBP files using Microsoft Access. The resulting database was called the "USGS Bat Banding Database." I created three different tables of information: (1) bander name and contact information; (2) initial banding information; and (3) recapture information (fig. 6). A table is database terminology for a collection of data about a specific topic and is organized into columns, also called fields, and rows, or records. By using a separate table for each topic, the data are stored only once, which makes a database more efficient and reduces data-entry errors. The bander information table includes name (first, middle initial, and last), address, title, phone number, and email address. A unique identification number (BanderID) is automatically created when a new bander is entered into the database. This BanderID links to the table of initial banding. The initial banding table includes band number, species, sex, locality name, site name, county, State, date, and a check box for whether the bat was ever recaptured. Recaptured is the generic name used for dead recovery, return, resight, or recapture. If the box indicating "bat was recaptured" is checked, the final table of recapture information needs to be completed. The recapture table includes the band number (BandNumber), type of recapture, locality, site name, county, State, date, person reporting the recapture, and BanderID. The three tables in the database are all linked by BanderID and BandNumber.

I entered Senger's entire set of banding cards located in the BBP files into this relational database. I then queried the database and created summary statistics and reports for the eight species of bats banded from 1964 to 1975. I created summaries by species and location. The resulting summaries were then compared to Senger's data originally coded onto punch cards then transferred to disks. He provided me with two data files of his banding efforts, one sorted by bat band number, and another sorted by date, but with the complete banding information located in each of these files. The files were in an unknown database format, which I then converted to Microsoft Excel spreadsheets and sorted by species, sex, band number, and location.

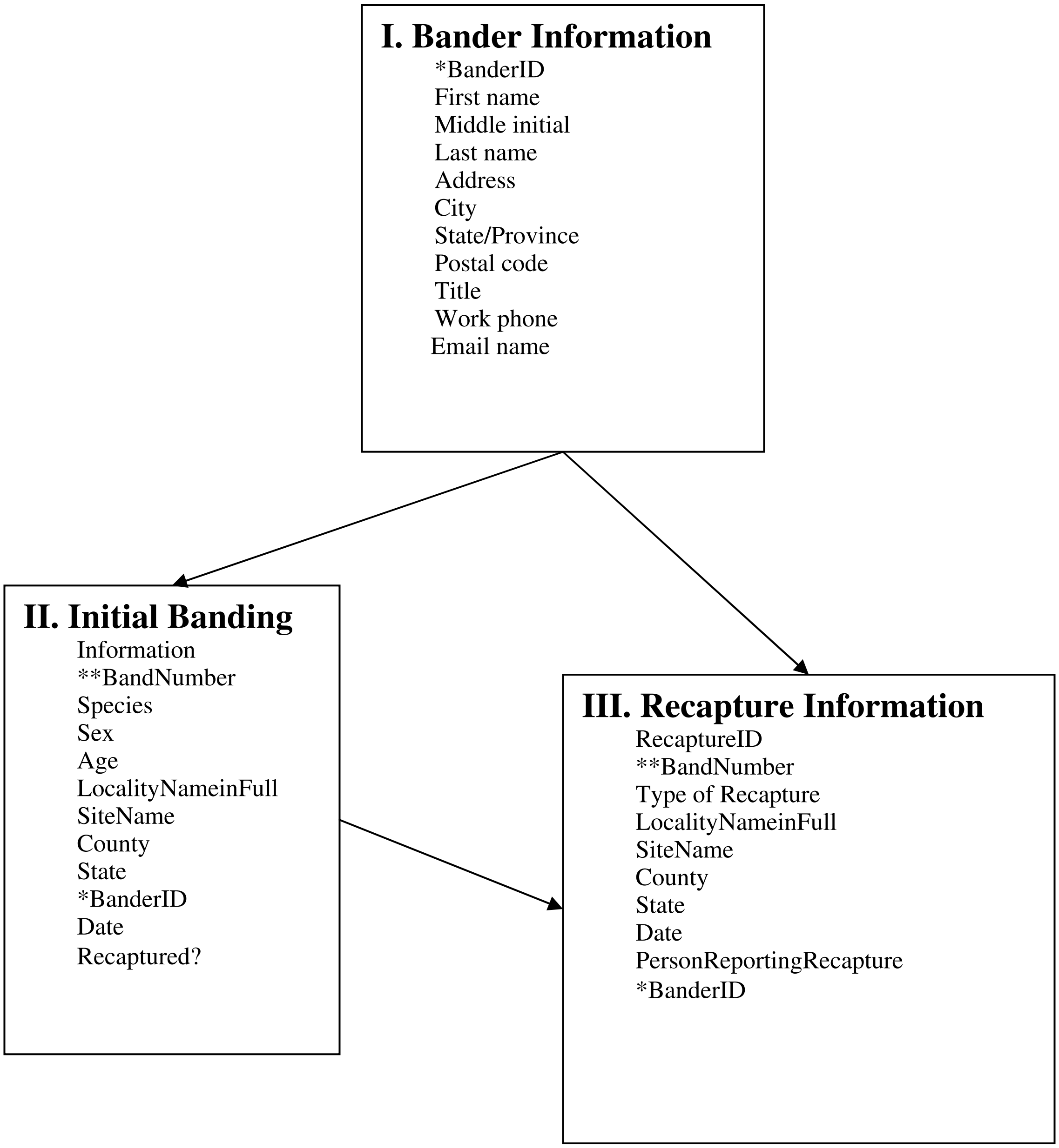


Figure 6. Data forms for the three tables in the U.S. Geological Survey Bat Banding Database and how they are linked. The arrows represent a "one-to-many" link. *The Bander Information table (I) is linked to many Initial Banding records (II) with the unique BanderID. **The Initial Banding records (II) are linked to Recapture Information (III) by a unique BandNumber.

Survival Analysis

I chose three general areas in three counties in the State of Washington to examine annual survival and capture probabilities for Townsend's big-eared bats banded from 1964 to 1975 (fig. 7). Adult male and female bats were banded in the fall and winter by Senger in their hibernacula (all hibernacula were caves). In southwestern Washington, the two cave areas were the Mount St. Helens area and Klickitat County. The Mount St. Helens area consisted of bats hibernating in two main caves, Bat Cave and Spider Cave, both in Skamania County (hereinafter, this site will be called Skamania). The Klickitat County site consisted of bats hibernating in two main caves, Jug Cave and Poacher's Cave (hereinafter, this site will be called Klickitat). In northwestern Washington, Skagit County, most of the Townsend's big-eared bats were banded at Blanchard Mountain Cave, now called Senger's Talus Cave (hereinafter, this site will be called Skagit). Bats were typically banded in November or December.

Figure 7. A map of the State of Washington with the three main counties where C.M. Senger and associates banded hibernating Townsend's big-eared bats from 1965 to 1981. The three counties are Skagit in the northwest, and Klickitat and Skamania in the southwest. Specific locations of the caves within these counties used in the survival analysis are not displayed to protect their valuable resources (Federal Cave Resources Protection Act, December 1988).

I created separate yearly capture (encounter) history files for Townsend's big-eared bats for each of the three locations (Skamania, Klickitat, and Skagit). I considered the two caves in the Mount St. Helens area, Bat Cave and Spider Cave, as one population of wintering bats. These two caves formed the main hibernating populations and bats sometimes moved between them in the winter months (C.M. Senger, oral commun., 2008)). I also considered colonies occupying the two main caves where banding took place in Klickitat County as one population of wintering bats. There was only one main cave where banding took place in northwestern Washington, so that was the third population of wintering bats used for survival analysis. If a bat was captured once during the winter, it was coded as "1" in the encounter file even if it was captured or resighted multiple times during the winter. A bat was coded as a "0" for that year if it was not recaptured during that winter. In Skamania, banding of bats occurred from December 1965 through November 1970 with recaptures noted until the winter of 1980 (16 years of capture occasions). For Klickitat, banding of bats occurred from November 1968 through October 1975 with recaptures noted until the winter of 1976 (9 years of capture occasions). For Skagit, banding took place from winter of 1965 through winter of 1973 with recaptures noted until the winter of 1977 (14 years of capture occasions).

I used the "recaptures only" model in Program MARK to analyze the mark-recapture data for Townsend's big-eared bats (White and Burnham, 1999; software available online at *http://www/phidot.org/software/mark/docs/book/*). The "recaptures only" model in Program MARK is the open population model based on Cormack-Jolly-Seber (CJS) (Cormack, 1964; Jolly, 1965; Seber, 1965). The CJS model requires information on only the recaptures of the marked animals and that the marked animals are representative of the population (Amstrup and others, 2005). The parameters of interest are apparent survival, ϕ, and capture probability, *p*. Apparent survival is not equivalent to survival but is the probability that the animal is alive and remains on the study area and is available for recapture. The CJS method cannot distinguish mortality from permanent emigration. I made the following specific assumptions based on the general assumptions in Williams and others (2002): (1) every banded bat present in the population at sampling period i has the same probability p_i of being recaptured; (2) every banded bat present in the population immediately following the sampling in period i has the same probability ϕ_i of survival until sampling period $i + 1$; (3) bands were neither lost or overlooked and were recorded correctly; (4) sampling periods were short periods (1–2 days of banding in November or December of each winter banding occurred) and banded bats were released immediately; (5) all emigration from the caves was permanent; and (6) the fate of each banded bat was independent of the fate of any other bat with respect to capture and survival probability.

I constructed a set of *a priori* candidate models to investigate survival and capture probabilities for the three wintering populations of bats (table 6). Candidate models examined the effects of time and sex on both survival and capture probabilities. For models incorporating time, each parameter was allowed to differ for each year in a nonlinear, random pattern. I also examined whether there was an increasing or decreasing linear trend on survival and capture probabilities over the course of the winter banding activities. The global model included sex and time-varying differences on both survival and capture probabilities. I ran the global model first, and then constrained survival and capture probabilities as either constant over time, different by sex, or with a downward (or upward) trend. A total of 38 models were built in Program MARK for each of the three locations.

I used the information-theoretic approach to compare these different candidate models (Burnham and Anderson, 2002). I assessed the goodness of fit (GOF) of the global model and whether the encounter data were overdispersed using the median $\hat{c}$ in Program MARK. The most parsimonious set of models was selected using a combination of QAICc (Akaike's Information

Table 6. Parameter combinations used in modeling survival and capture probabilities of wintering Townsend's big-eared bats in three locations in Washington. All bats were banded in the winter from 1964 to 1975 by C.M. Senger and associates. Model nomenclature follows the format suggested by Lebreton and others (1992).

Model description	Parameters
General model (survival and capture probabilities differed by time and sex)	ϕ (sex × time) p (sex × time)
Capture	
Constant over time	p (.)
Constant over time, but differed by sex	p (sex)
With an increasing (or decreasing) trend	p (trend)
Differed by sex and with an increasing (or decreasing) trend	p (sex + trend)
Different every year	p (time)
Survival	
Constant over time	ϕ (.)
Constant over time, but differed by sex	ϕ (sex)
With an increasing (or decreasing) trend	ϕ (trend)
Differed by sex and with an increasing (or decreasing) trend	ϕ (sex + trend)
Different every year	ϕ (time)

Criterion corrected for overdispersed data and small sample sizes), $\Delta QAIC_c$, and $QAIC_c$ weights (Burnham and Anderson, 2002). I used model averaging techniques to calculate the real estimates of apparent survival and capture probabilities for each location. Model averaging computes the average of a parameter from all models in the model set and therefore includes model selection uncertainty in the estimate of precision of the parameter. Model averaging produces unconditional estimates of variances and standard errors (Burnham and Anderson, 2002). I examined the confidence intervals around the beta (β) estimate for a trend in survival and capture probabilities. If the 95-percent confidence intervals for the $\hat{\beta}$ for trend did not include 0, I considered this as additional support that the trend covariate had an effect on survival and capture probabilities.

Results

Database Management

I entered 1,943 banding cards into the USGS Bat Banding Database. On these cards, there were 1,222 recaptures of banded bats. Many of the recaptures were multiple captures of the same individuals through the years. Of the total initially banded, 560 individuals were recaptured at least once. A total of 3,165 individual database records were entered (initial banding information plus recapture events). This took approximately one and a half weeks of data-entry time (60 hours).

Eight different species of bats were banded from October 24, 1964, through December 24, 1975, in seven counties in Washington with information on recaptures collected until November 10, 1980, (table 7). No new bats were banded after December 28, 1975.

There were a few discrepancies between Senger's bat-banding cards located in the BBP files and his original data files, but these discrepancies were minor (table 7). The dates he conducted banding were identical between the two sets of data. However, the dates of reported recoveries and recaptures were slightly different. The card files contained information on recoveries/recaptures from January 1, 1965, through November 23, 1979, whereas his original data contained information on recaptures spanning November 21, 1964, and November 10, 1980. This latter discrepancy was probably due to a few recaptures failing to be reported to the BBP. There were slight differences in the total number of bats banded by species; in some cases, the BBP files seemed more complete and in some cases Senger's original data were more complete (table 7). In other cases, there were some missing bands in Senger's information located in the BBP files but were not missing in Senger's original data files. For example, bands including the series BAT5-23736 to BAT5-23738 were never applied according to the Senger's cards in the BBP files but were applied to bats according to what he had on file. Also, for the series including BAT6-10201-10205, there was no indication of bands being applied in Senger's files; however there were three recapture records (cards) on file in the BBP files for BAT6-10203.

Table 7. A comparison of information for Clyde M. Senger's banding efforts in Washington from fall of 1964 through winter of 1975. I compared the information contained in the BBP files (and entered into the USGS Bat Banding Database) to original database information entered and maintained by Senger, the bander. Total number of species banded by sex (AM = Adult Males, AF = Adult Females) and number of recaptures are compared between the "BBP Files" and "Senger's Original Data."

	Bat Banding Program files		**Senger's original data**	
Species banded	**Total number banded (AM:AF)**	**Number recaptured (AM:AF)**	**Total number banded (AM:AF)**	**Number recaptured (AM:AF)**
Townsend's big-eared bat	1,346 (560:786)	517 (178:339)	1,333 (567:766)	518 (179:339)
Big brown bat	23 (8:15)	1(1:0)	24 (10:14)	1 (1:0)
California myotis	1 (adult, unknown sex)	0	1 (1:0)	0
Long-eared myotis	103 (96:7)	4 (3:1)	102(95:7)	4 (3:1)
Little brown myotis	255 (233:22)	13 (13:0)	259 (238:21)	13 (13:0)
Fringed myotis	1 (1:0)	0	1 (1:0)	0
Long-legged myotis	136 (116:20)	9 (8:1)	137 (118:19)	11 (10:1)
Yuma myotis	78 (65:13)	1 (1:0)	80 (67:13)	3 (3:0)

Survival Analysis

Not all Townsend's big-eared bats banded were used in the survival analyses. I used 1,123 Townsend's big-eared bats banded at the three main locations for analyses. More female bats were banded than males with an overall sex composition of 57.7 percent females and 42.3 percent males (table 8). The most bats were banded at Spider Cave (405) with 53.3 percent females. A total of 378 bats were banded at Bat Cave with 58.5 percent of them female. Sex ratios were more skewed

Table 8. Number of Townsend's big-eared bats used in survival analyses, by county, cave, and sex. All bats were banded in the winter from 1964 to 1975 by Clyde M. Senger and associates with recaptures noted until winter of 1980. AM = Adult Males, AF = Adult Females.

County	Cave name	Year of banding	Reports of bands applied (AM:AF)
Skamania	Bat Cave	1966	228 (91:137)
		1967	31 (13:18)
		1968	24 (6:18)
		1969	52 (26:26)
		1970	43 (21:22)
	Spider Cave	1965	268 (133:135)
		1966	84 (32:52)
		1967	22 (10:12)
		1968	5 (3:2)
		1969	20 (9:11)
		1970	6 (2:4)
Klickitat	Jug Cave	1968	32 (6:26)
		1969	47 (20:27)
		1970	11 (7:4)
		1971	13 (4:9)
		1972	3 (0:3)
		1973	1 (0:1)
		1975	3 (0:3)
	Poacher's Cave	1968	8 (0:8)
		1969	31 (6:25)
		1970	49 (19:30)
		1971	7 (5:2)
		1972	2 (1:1)
		1973	1 (1:0)
Skagit	Blanchard Mountain Cave (Senger's Talus Cave)	1965	49 (20:29)
		1966	18 (8:10)
		1967	13 (7:6)
		1968	19 (9:10)
		1969	13 (5:8)
		1970	8 (5:3)
		1971	5 (2:3)
		1972	1 (0:1)
		1973	6 (4:2)
Totals			1,123 (475:648)

toward females in Klickitat County. Of 110 banded bats at Jug Cave, 66.4 percent were female, and 67.3 percent of 98 banded at Poacher's Cave during six winters were female. Farther north in Skagit County, at Blanchard Mountain Cave (Senger's Talus Cave), 54.5 percent of the 132 banded bats during the eight winters of banding were female. All banded bats used for these analyses were considered adults of unknown age but likely included some young-of-the-year.

For each location, estimates of annual apparent survival and capture probabilities varied somewhat by sex, but these differences were not significant (table 9). Apparent survival for male Townsend's big-eared bats ranged from a low of 0.54 for Klickitat County to a high of 0.68 for Skagit County. Apparent survival for adult female Townsend's big-eared bats ranged from a low of 0.60 for Skamania County to a high of 0.67 for Skagit County. Adult male bats tended to have lower capture probabilities than females, ranging from a low of 0.30 in Klickitat to a high of 0.46 for Skamania. Capture probabilities for females ranged from 0.49 in both Klickitat and Skamania to 0.61 in Skamania. There were no significant differences between the sexes and among the locations in the survival estimates; all six 95-percent confidence intervals around the apparent survival were broadly overlapping. Capture probabilities also did not differ significantly between sexes and among locations (95-percent confidence intervals also overlapped).

No clear top model was chosen with the model-selection techniques for each of the three locations (counties). However, a trend on either apparent survival or capture probabilities was always in at least one of the three top models (tables 10–12). The three top models in all three analyses explained more than 60 percent of the model variation. Although 38 models were constructed in Program MARK for each analysis, I included only the models within 10 $\Delta QAIC_c$ of one another and the global model for reference in the tables of model results (tables 10–12). Therefore, the total number of models displayed in these tables varies by county.

The highest ranking model for Skamania County was a model with an upward trend on apparent survival and differences in capture probabilities by sex (table 10). The confidence

Table 9. Maximum likelihood estimates of apparent survival ($\hat{\phi}$) and capture probabilities (p) with associated standard errors (SE) and 95-percent confidence intervals (95% CI) for Townsend's big-eared bats by county and sex. All bats were banded in the winter from 1964 to 1975 by C.M. Senger and associates with recaptures noted until winter of 1980. Estimates were calculated from model {ϕ (sex) p (sex)}.

County	Sex	$\hat{\phi}$ ± SE (95% CI)	$\hat{p}$ ± SE (95% CI)
Skamania	Male	0.58 ± 0.04 (0.51–0.65)	0.46 ± 0.06 (0.35–0.56)
	Female	0.60 ± 0.03 (0.54–0.65)	0.61 ± 0.04 (0.52–0.69)
Klickitat	Male	0.54 ± 0.11 (0.33–0.75)	0.30 ± 0.12 (0.12–0.57)
	Female	0.65 ± 0.05 (0.54–0.74)	0.49 ± 0.07 (0.35–0.63)
Skagit	Male	0.68 ± 0.04 (0.59–0.76)	0.40 ± 0.06 (0.29–0.52)
	Female	0.67 ± 0.04 (0.59–0.73)	0.49 ± 0.06 (0.39–0.60)

Table 10. Results from Program MARK for modeling survival (ϕ) and capture probabilities (p) of adult female and male Townsend's big-eared bats roosting in hibernacula in Skamania County, Washington, from band-recapture data collected from 1964 to 1980. For each model I list the model name, the Akaike Information Criterion corrected for overdispersion ($QAIC_c$), the $\Delta QAIC_c$, $QAIC_c$ weight, and number of parameters (*K*). The model with the lowest $QAIC_c$ is in boldface type. Data were collected by C.M. Senger and associates. See table 6 for description of model variables.

Model name	$QAIC_c$	$\Delta QAIC_c$	$QAIC_c$ weight	*K*
ϕ (trend) *p* (sex)	**992.43**	**0.00**	**0.29**	**4**
ϕ (trend) *p* (sex + trend)	992.59	0.16	0.26	5
ϕ (sex + trend) *p* (sex + trend)	994.13	1.69	0.12	6
ϕ (.) *p* (sex)	994.85	2.42	0.08	3
ϕ (trend) *p* (trend)	995.28	2.85	0.07	4
ϕ (sex + trend) *p* (trend)	995.30	2.87	0.07	5
ϕ (trend) *p* (.)	996.16	3.72	0.04	3
ϕ sex) *p* (sex)	996.71	4.28	0.03	4
ϕ (trend) *p* (.)	996.16	4.43	0.03	3
ϕ (.) *p* (.)	998.92	6.49	0.01	2
ϕ (sex) *p* (.)	999.32	6.89	0.01	3
ϕ (.) *p* (trend)	1,000.37	7.94	0.01	3
ϕ (sex × time) *p* (sex × time)	1,063.78	71.35	0.00	58

intervals around the β estimate for a trend on survival did not include 0 indicating a significant upward trend [$\hat{\beta}$ = 0.07 ± 0.03 SE (0.004–0.14 95-percent CI)]. Female big-eared bats had a higher capture probability than males [$\hat{p}$ = 0.62 ± 0.04 SE (0.54–0.71 95-percent CI) for females; $\hat{p}$ = 0.46 ± 0.05 SE (0.36–0.57 95-percent CI) for males]. Since there appeared to be quite a bit of model uncertainty with three of the top models within two $\Delta QAIC_c$ of one another and explaining 67 percent of the variation, I calculated model-averaged estimates of apparent survival and capture probabilities (fig. 8).

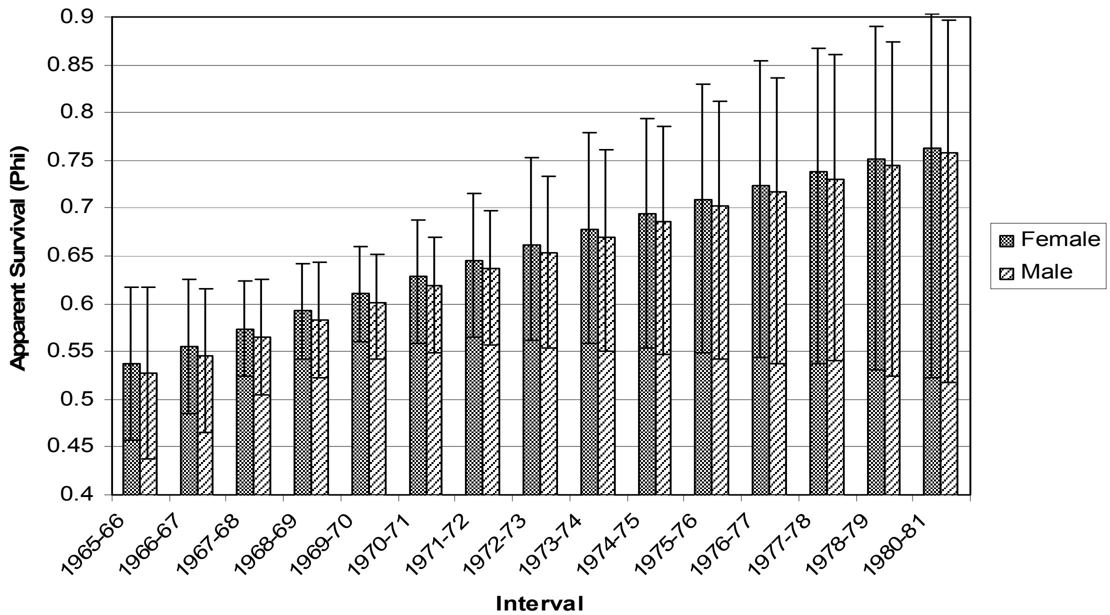
The highest ranking model for the Klickitat County was the model with a constant apparent survival and a downward trend in capture probabilities (table 11). The confidence intervals around the β estimate for the trend on capture probabilities did not include 0, indicating a significant, downward trend [$\hat{\beta}$ = –0.43 ± 0.11 SE (–0.66 to –0.20 95-percent CI)]. The estimate for apparent survival was 0.69 ± 0.06 SE (0.56–0.79 95-percent CI). As with the Skamania analysis, there appeared to be quite a bit of model uncertainty, with five of the top models within two $\Delta QAIC_c$ of one another and the top three explaining 70 percent of the variation. Therefore, I calculated model-averaged estimates of apparent survival and capture probabilities (fig. 9).

Table 11. Results from Program MARK for modeling survival (ϕ) and capture probabilities (p) of adult female and male Townsend's big-eared bats roosting in hibernacula in Klickitat County, Washington, from band-recapture data collected from 1964 to 1980. For each model I list the model name, the Akaike Information Criterion corrected for overdispersion ($QAIC_c$), the $\Delta QAIC_c$, QAICc weight, and number of parameters (K). The model with the lowest $QAIC_c$ is in boldface type. Data were collected by C.M. Senger and associates. See table 6 for description of model parameters.

Model name	$QAIC_c$	$\Delta QAIC_c$	$QAIC_c$ weight	K
ϕ (.) p (trend)	**270.56**	**0.00**	**0.24**	**3**
ϕ (sex + trend) p (trend)	270.59	0.03	0.24	5
ϕ (trend) p (sex + trend)	270.69	0.13	0.22	5
ϕ (sex + trend) p (sex + trend)	272.18	1.62	0.11	6
ϕ (trend) p (trend)	272.28	1.72	0.10	4
ϕ (.) p (time)	273.56	3.00	0.05	9
ϕ (trend) p (sex)	276.48	5.92	0.01	4
ϕ (time) p (time)	277.25	6.70	0.01	12
ϕ (trend) p (.)	279.06	8.50	0.00	3
ϕ (.) p (sex)	279.65	9.09	0.00	3
ϕ (time) p (sex)	279.80	9.25	0.00	9
ϕ (.) p (sex × time)	280.03	9.47	0.00	15
ϕ (sex) p (.)	280.47	9.92	0.00	3
ϕ i (sex × time) p (sex * time)	288.80	18.24	0.00	21

Table 12. Results from Program MARK for modeling survival (ϕ) and capture probabilities (p) of adult female and male Townsend's big-eared bats roosting in hibernacula in Blanchard Mountain Cave (Senger's Talus Cave), Skagit County, Washington, from band-recapture data collected from 1964 to 1980. For each model I list the model name, the Akaike Information Criterion corrected for overdispersion ($QAIC_c$), the $\Delta QAIC_c$, $QAIC_c$ weight, and number of parameters (*K*). The model with the lowest $QAIC_c$ is in boldface type. Data were collected by C.M. Senger and associates. See table 6 for description of model parameters.

Model name	**$QAIC_c$**	**$\Delta QAIC_c$**	**$QAIC_c$ weight**	***K***
ϕ (.) *p* (time)	**602.66**	**0.00**	**0.26**	**13**
ϕ (.) *p* (trend)	602.73	0.07	0.25	3
ϕ (trend) *p* (trend)	604.64	1.98	0.09	4
ϕ (sex) *p* (time)	604.78	2.12	0.09	14
ϕ (.) *p* (.)	605.49	2.83	0.06	2
ϕ (trend) *p* (sex + trend)	605.94	3.28	0.05	5
ϕ (.) *p* (sex)	606.06	3.39	0.05	3
ϕ (sex + trend) *p* (trend)	606.59	3.94	0.04	5
ϕ (trend) *p* (.)	607.68	4.43	0.03	3
ϕ (sex) *p* (.)	607.42	4.76	0.02	3
ϕ (trend) *p* (sex)	607.68	5.02	0.02	4
ϕ (sex + trend) *p* (sex + trend)	608.04	5.38	0.02	6
ϕ (sex) *p* (sex)	608.11	5.45	0.02	4
ϕ (time) *p* (time)	612.65	9.98	0.00	21
ϕ (sex × time) p (sex × time)	668.49	65.83	0.00	49



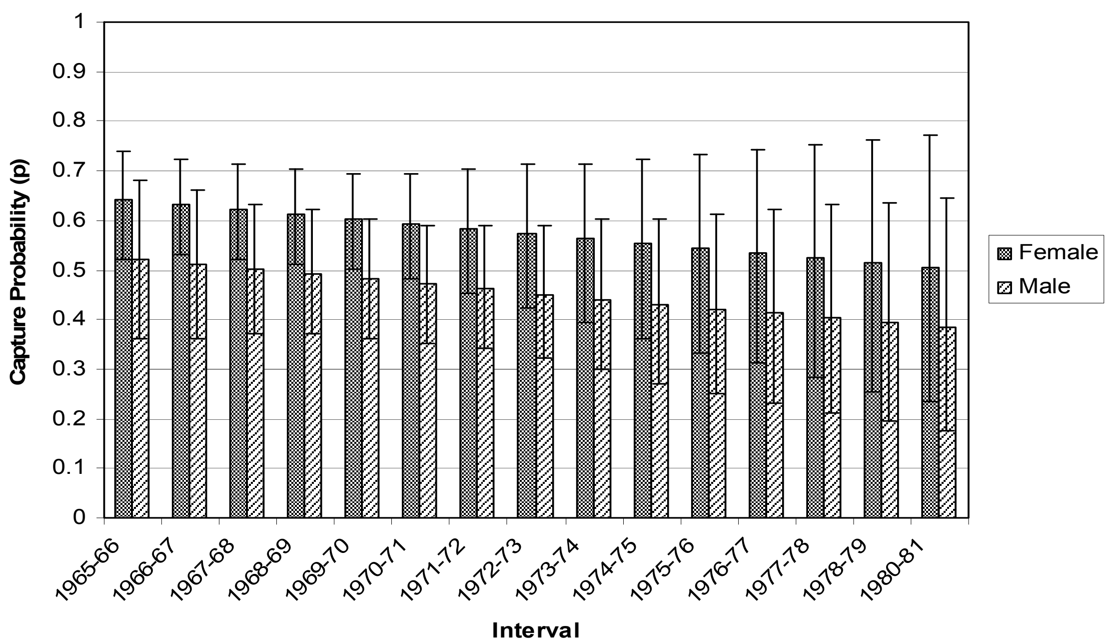
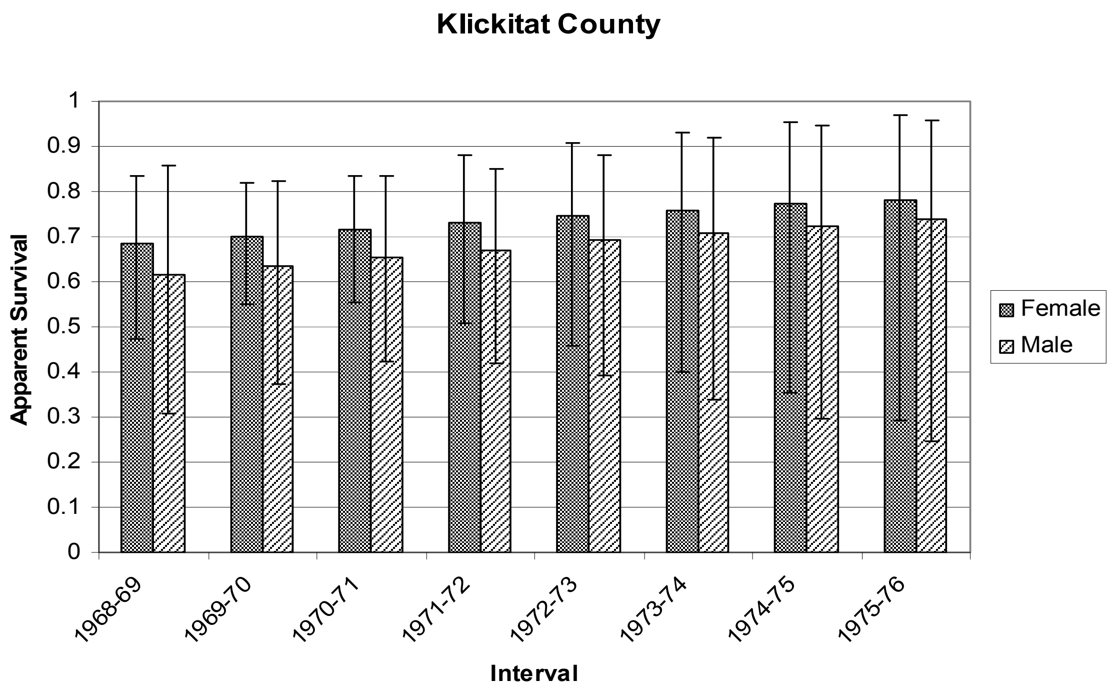


Figure 8. Model averaged estimates of apparent survival and capture probabilities for Townsend's big-eared bats hibernating in Skamania County, Washington, from 1965 to 1981. Error bars are 95-percent confidence intervals.



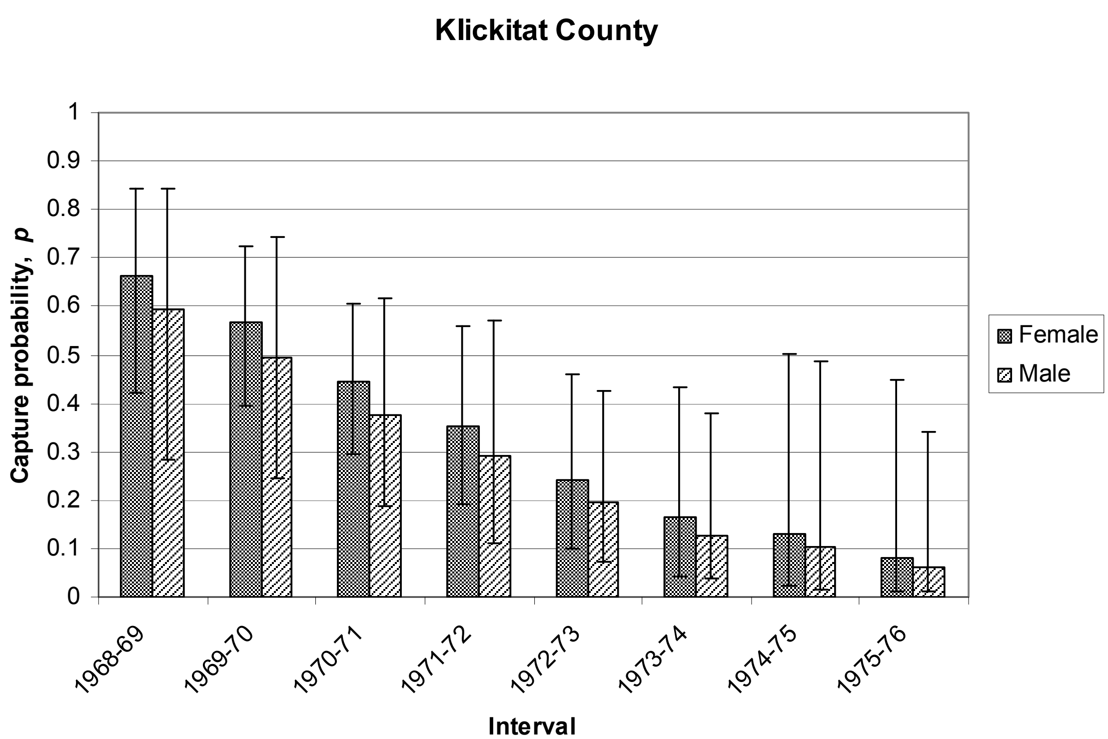


Figure 9. Model averaged estimates of apparent survival and capture probabilities for Townsend's big-eared bats hibernating in Klickitat County, Washington, from 1968 to 1976. Error bars are 95-percent confidence intervals.

The highest ranking model for Skagit County was the model with a constant apparent survival and capture probabilities differing by year (not linear trend) (table 12). However, the confidence intervals around the β estimate for the trend on capture probabilities did not include 0, indicating a significant downward trend [$\hat{\beta}$ = –0.12 ± 0.05 SE (–0.22 to –0.01 95-percent CI)]. The estimate for apparent survival was 0.68 ± 0.03 SE (0.62–0.74 95-percent CI). As with the other two analyses, there appeared to be quite a bit of model uncertainty with the three top models within two $\Delta QAIC_c$ of one another and explaining 60 percent of the variation. Therefore, I calculated model-averaged estimates of apparent survival and capture probabilities (fig. 10).

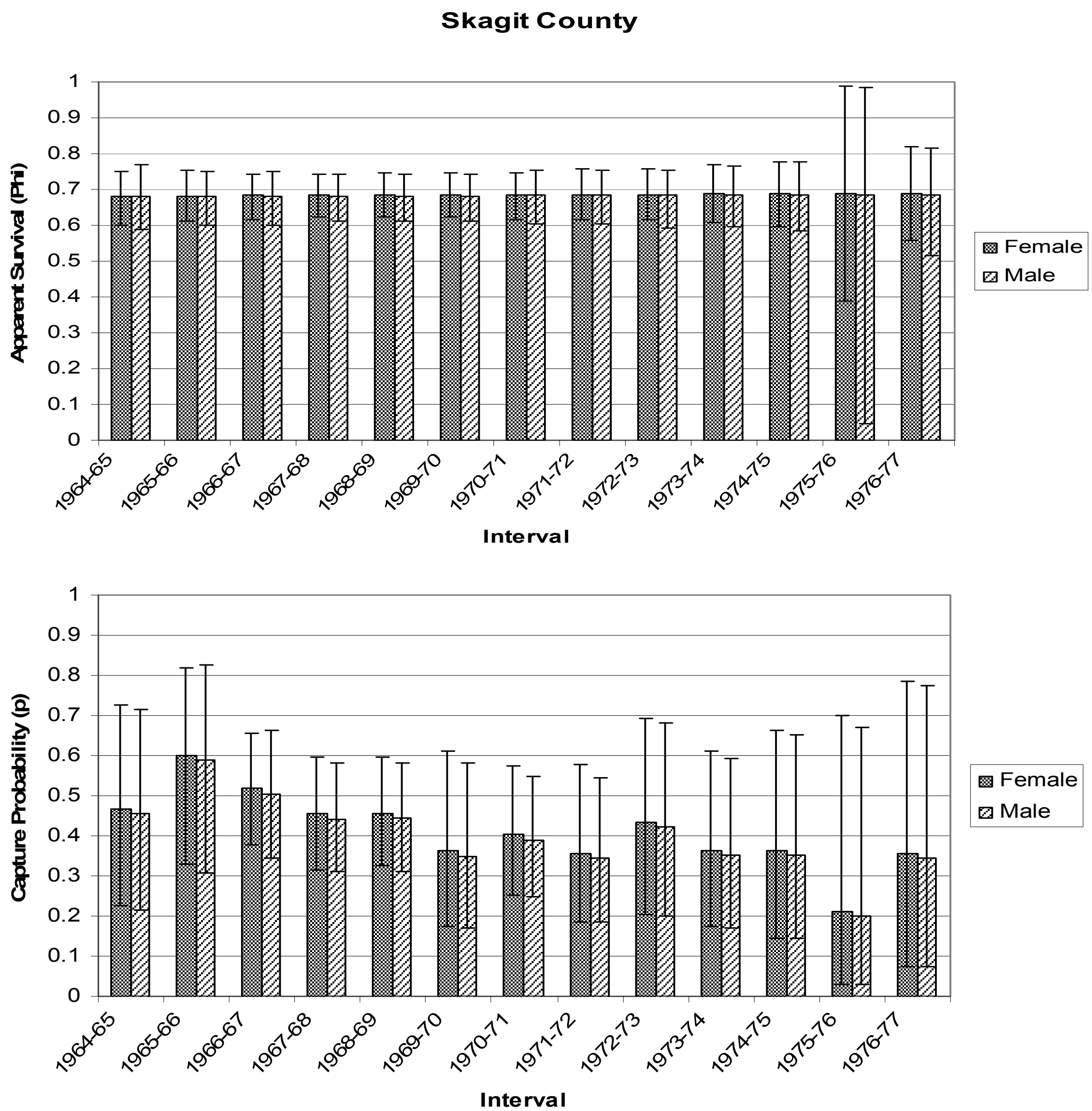


Figure 10. Model averaged estimates of apparent survival and capture probabilities for Townsend's big-eared bats hibernating in Blanchard Mountain Cave (Senger's Talus Cave), Skagit County, Washington, from 1964 to 1977. Error bars are 95-percent confidence intervals.

Discussion

Estimates of apparent annual survival of wintering Townsend's big-eared bats in three locations in Washington ranged from as low as 53.5 percent to as high as 76.0 percent (from the models incorporating trend and sex differences). Estimates of capture probability also varied by location, time, and sex, ranging from a low of 8.1 percent to a high of 75.0 percent. Assuming a constant survival probability over time and trend, survival ranged from a low of 54 percent for adult males in Klickitat County to a high of 68 percent for males in Skagit. Female survival ranged from a low 60 percent in Skamania County to a high of 67 percent in Skagit County. In Skamania and Klickitat Counties, male survival tended to be lower than female, but these differences were not significant. In Skagit, male and female survival probabilities were similar (68 and 67 percent respectively). Assuming constant survival and using regression techniques, Senger estimated survival to be about 58 percent (both sexes) per year (unpublished presentation to the American Society of Mammalogists, June 21, 1971). In a later publication, he estimated 60 percent of the banded bats survived each year to be recaptured later (Senger, 1973). These estimates derived by Senger did not have an associated error estimate but were similar to the estimates I derived 35 years later using Program MARK and maximum likelihood techniques. However, the estimates I provide include associated variance and confidence intervals. I was also was able to examine trends, time effects, and sex differences in survival as well as capture probabilities at each of the three locations where banding took place. At all three hibernating locations, more than 60 percent of the variation in survival and capture of Townsend's big-eared bats was explained by a combination of differences between the sexes and time or trend differences.

Pearson and others (1952) investigated natural history and reproduction of Townsend's big-eared bats in California from 1947 to 1951. They used the percentage of recaptured banded bats to calculate annual return rates of 40–54 percent for juveniles and annual return rates of 70–80 percent for adult females. These estimates were from females in nursery colonies. The adult female return rate of 70–80 percent was higher than the estimates I calculated for wintering female bats (60–70 percent), however there was no associated variance and precision associated with these annual return rates. Pearson and others (1952) also banded bats in the winter at caves in the Mt. Lassen area and recovered 53 percent of the males and 58 percent of the females in two subsequent years. These return rates are more similar to survival estimates I obtained for wintering bats in Washington, but again there were no estimates of variance or precision associated with the California return rates. As far as I know, no other estimates of survival exist for Townsend's big-eared bats besides the results reported in this document and the work of Pearson and others (1952) and Senger's rough estimate (Senger, 1973).

CJS-based survival estimates of other species of bats varied in their precision compared to the estimates I calculated for wintering Townsend's big-eared bats in Washington. Keen and Hitchcock (1980) used CJS-based models to estimate survival for wintering little brown myotis in Ontario. They found mean survival rates of 0.816 ± 0.010 (SE) and 0.807 ± 0.022 for males and females, respectively. The standard errors associated with this study were small compared to the standard errors I estimated for Townsend's big-eared bats (standard errors ranged from a low of 0.03 to a high of 0.11; table 9). This was probably due to the much larger sample sizes banded during the study in Ontario. Nearly 2,000 little brown myotis were banded from 1947 to 1962 and recaptures noted until 1975. In another study, Hitchcock and others (1984) estimated survival rates in eastern small-footed bats and big brown bats in southeastern Ontario by using the CJS modeling approach. Annual survival of eastern small-footed bats was 0.757 ± 0.111 and 0.421 ± 0.071 for males and females, respectively. For big brown bats, annual survival was estimated to be 0.697 ± 0.061 and 0.465 ± 0.061 for males and females, respectively. The standard errors for these estimates were larger than the standard errors I calculated for Townsend's big-eared bats, and this was likely due to the smaller sample sizes banded and recaptured from 1941 to 1948 during the study in southeastern Ontario.

Although I was able to apply current mark-recapture theory successfully to Senger's data on bats banded during the BBP, there are several major caveats that need to be addressed when interpreting the results from this retrospective analysis. An overall assumption of mark-recapture theory is that the method used to mark individuals should not harm them and thereby potentially negatively affect survival. If marking negatively affects bats, the conclusions drawn from the marked sample cannot be extrapolated to the population. The specific assumptions I made for this analysis were the following: (1) Every banded bat present in the population at sampling period *i* has the same probability p_i of being recaptured; (2) every banded bat present in the population immediately following the sampling in period *i* has the same probability ϕ_i of survival until sampling period $i + 1$; (3) bands were neither lost or overlooked, and were recorded correctly; (4) sampling periods were short periods (1–2 days of banding in November or December of each winter banding occurred) and banded bats were released immediately; (5) all emigration from the caves was permanent; and (6) the fate of each banded bat was independent of the fate of any other bat with respect to capture and survival probability. Assumptions (1), (2), and (6) relate to the marked sample. Assumptions (3) and (4) did not appear to have been violated. During discussions with Senger, he indicated that bands did not appear to be lost and that information on the band was very carefully recorded. For assumption (4), sampling periods during each winter occurred over 1–2 days, which is considered short relative to the interval over which survival was estimated (annual survival was estimated).

I will discuss two critical concerns: band injuries and emigration [assumption (5)]. Banding and research negatively affected Townsend's big-eared bats hibernating in these areas in several different ways (C.M. Senger, oral commun., 2008; Senger, 1969, 1973, 1985; Senger and Crawford, 1984). Senger noted band injuries of Townsend's big-eared bats over the course of his banding efforts. Of 278 bats he had banded 2 years previously (in 1966) with No. 2 bands, one of 21 recaptures had a cut through the wing membrane from the band, and one other recapture had some swelling. On the other hand, nearly one-half of the 28 recaptures from 210 bats banded in the previous year (1967) with the "BAT series" bands had cuts through the wing membranes, although without significant swelling or scar tissue formation. Humphrey and Kunz (1976) also documented band injuries in this species. They studied Townsend's big-eared bats in the southern Great Plains (western Oklahoma and Kansas) and examined population ecology of the bats using banded individuals. They found evidence of in-grown bands, chewed bands, and infected arms 1 and 2 years after banding. Some bats would exhibit all three of these conditions simultaneously. They concluded that this species responds negatively to the presence of the band more strongly than any other temperate zone species on which they had conducted mark-recapture studies (Humphrey and Kunz, 1976).

Sometimes banding would cause bats to move to another cave. For example, on January 1, 1970, a number of bats were banded at Bat Cave in Skamania County, and on that same day, a number of these were again resighted at Prince Albert Cave, also in Skamania County. This movement could be considered temporary emigration and would bias the survival and capture probability estimates. None of the bats I used in the analysis appeared to move temporarily to known caves in the area; however, bats could have moved temporarily to other unknown locations. Senger wrote to W.H. Davis and told him that he did not think that the recapture ratios were indicative of survival because bats seem to readily move from one cave to another when disturbed, and he did not think he was sampling all of the caves in the area (W.H. Davis, 1968). Two Townsend's big-eared bats were seen one afternoon in Bat Cave at 1,200 ft, but the next morning the same bats were seen at Flow and Spider Caves, which were both at an elevation of 2,800 ft and at least 4 miles away. Temperatures at the higher caves had been near freezing all day, and it was snowing. Early in the evening it cleared up and the temperature dropped from –1 degree Celsius to –3.6 degrees. Senger was surprised that the bats had moved so far under such conditions and wondered how many fail to survive such movements when disturbed by banding or other research activities. He measured the weight loss for the bats which had moved: a 12.76-g male lost 0.46 g; a 10.59-g male lost 0.21 g; and a 13.86-g female lost 0.16 g (W.H. Davis, 1968).

The total number of bats in Spider Cave had declined markedly since the start of the study in 1965 with only 45 females and 22 males being found in 1967–68. A similar pattern of population decline was also noted for Bat Cave (Senger, 1969). Senger felt strongly that his study had been a serious disturbance to the bats, and he planned to reduce his visits for the next several years to preserve the remaining populations. Despite apparent population declines of bats in the area around Mount St. Helens, the capture probabilities in caves of Skamania County were unusually high for banded bats (fig. 7). Disturbance of the hibernating population at Spider Cave may have come from other sources as well. Spider Cave was relatively unknown by the public in the late 1960s but was located near a road and relatively accessible to the public (presentation on June 21, 1971, at the Annual Meeting of the American Society of Mammalogists, Vancouver, B.C.). About 100 acres of virgin timber were logged on the hillside just to the west of the mouth of Spider Cave in 1967, which may have had an effect on the use of the cave by bats. The hibernating populations of bats at Bat and Spider Caves appeared to recover somewhat from the drastic declines observed after the first few years of the banding efforts. In a 1984 unpublished report to the St. Helens Ranger District of the Gifford Pinchot National Forest, Senger reported that the hibernating populations at both Bat and Spider Caves had recovered somewhat, but to overall lower numbers than the original 250–300 counted. However, the observed population levels were consistent in the 6 years prior to 1984 (Senger and Crawford, 1984).

The examples of injuries due to banding and the potential for bats to move permanently out of the study area (or among different unknown caves within the study area) violated two of the assumptions of the CJS model. Direct injuries from bands and disturbance from banding violates the basic rule that the sampled and banded population is representative of the population at large. Movement of bats in response to banding activities could also violate the assumption of permanent emigration. Not all of the caves or other roost types were known for each area, otherwise movements could have been tracked using multistrata models (models that incorporate a transition probability in addition to survival and capture probabilities). Although none of the bats used in the analysis moved to other known caves besides Bat or Spider Caves, I cannot assume they did not permanently leave the area due to disturbance because not all possible cave locations were known. The number of bats that appeared to move among the Bat and Spider Caves was low, and if they did move, they were often seen at both caves during a single winter season. Only 8 of the 377 individuals banded from Bat Cave were recaptured at Spider Cave, and 19 of the 407 from Spider Cave were recaptured at Bat Cave. However low these numbers appear, additional movements most likely occurred that were not detected. These issues raise the questions: If a bat originally banded at Bat Cave was never captured again in succeeding winters, was that bat gone from the area, still in the area but in an unknown cave, dead from natural causes, or dead from negative effects of the marking technique? Violation of the assumption of permanent emigration does not always result in biased estimates of survival and capture probabilities, especially if the emigration is random (that is, every individual within an age-sex category has the same probability of being in the area exposed to sampling efforts; Williams and others, 2002).

Senger's banding data on mark-recapture of Townsend's big-eared bats in Washington was one of the most complete and well-maintained datasets examined in the BBP files. Resulting annual survival estimates from these data were relatively precise and modeling provided evidence of trends in survival, time effects, and differences in survival between the sexes. These results provide historical, *post hoc* estimates of an important life-history parameter for this species of bat wintering in caves in three localized areas. This dataset most likely represents the best possible set of banding cards in BBP files available for retrospective analysis that has not already been published elsewhere. Although this current analysis is important and provides the only CJS-based estimates of survival for the Townsend's big-eared bat that I am aware of, the quality of other BBP files and the value of the results do not justify the computerizing of all the remaining banding records to conduct *post hoc* survival analysis for other species and locations. This dataset was very clean, records were maintained well by both the bat bander and the BBP filing process, recaptures were high, and there appeared to be no band loss from chewing or natural wear and tear. It is doubtful that any other datasets in the BBP files that have not already been published exist of the quality of Senger's dataset. The computerization of the entire BBP files, in my mind, would only serve as an interesting historical database for summarizing numbers of bats banded by location, species, age, and sex and would not be useful for large-scale mark-recapture analysis for survival (or any other population parameter).

Part 4. Summary of Problems, Recommendations, and Conclusions

Summary of Problems with the Bat Banding Program

(1) Problems with Bands

Numerous problems with the USFWS bat bands hampered the BBP during the entire tenure of the program. Early in the program, the aluminum USFWS bird bands applied to bats caused direct injuries. The sharp metal edges of the bird bands at the corners were found to cut into the wing membranes causing the flesh to grow over the ends of the band, tearing the wing membranes, causing infections, and could eventually even causing structural and bone damage. The resulting irritation from the sharp metal edges would also frequently cause the bats to chew on the bands, which would make the bands illegible and ruin any possibility for valid recoveries. The lipped "bat" bands developed in the mid-1950s did not solve the problems of injury and illegibility due to chewing. These new bands could cause more wing tears, and evidence of embedded bands and skeletal damage still occurred, but at a slower rate than with the bird bands. The degree of injuries witnessed by banders appeared to vary depending on the bat species. The bands themselves differed in the hardness of the aluminum alloy used in their manufacture. Some groups of bat bands were made with such a soft alloy, they were almost immediately rendered illegible from chewing or natural wear and tear. The style of numbering on the bands was also an issue; a few of the numbers stamped on the bands by the manufacturer were difficult to read even if one was an experienced bander. There was also evidence of duplication of USFWS bands. Not only were duplicate numbers of bands potentially applied to both birds and bats simultaneously, but there was evidence of duplicate bands applied to different individual bats. Due to these pervasive problems with bands, experimentation and testing of different styles of aluminum bands occurred during the entire BBP leading to major inconsistencies in the types of bands applied to bats. Overwhelming evidence of injuries to bats from bands was one of the main reasons for the moratorium on bat banding of 1973.

(2) Disturbance

During the BBP, bat banders and other researchers noticed significant population declines in bats and attributed some of these declines to research and disturbance by banding activities. One of the main motivations for the resulting banding moratorium of 1973 was anecdotal information on declines in 22 bat species in North America. The indirect negative effects of handling and observer influence associated with bat-banding activities was thought to be of greater magnitude than direct effects of injuries from bands. Banding often occurred during critically sensitive times such as hibernation and was implicated as one of the major causes of population declines in species that hibernate. Banding at maternity colonies in the summer could sometimes cause stress-induced abortion of fetuses. Disturbance could also cause bats to either temporarily move to alternative roosts or abandon a particular roost altogether. Declines in bat population due to banding activities were not unique to the BBP. Banding activities were discontinued in England, The Netherlands, and the Czech Republic due to substantial declines in the numbers of bats.

(3) Problems with the Bat Banding Program Files and Recoveries

The BBP was plagued with problems related to file management and reporting errors resulting in incomplete files and invalid recoveries. The validity of recoveries due to reporting errors was questioned throughout the program. The incomplete files were mostly a result of a lack of correspondence between banders and the BBP. For example, there was evidence that banders would often forget to return banding cards to the BBP. Banders would also not fill out the index cards (banding reports) completely. For instance, many index cards did not include the State, sex or species identification of banded bats. There was also evidence that bands were issued to one person, then handed down to someone else, and no information on this transaction was sent to the BBP. Errors often occurred in the filing process used by staff of the BBP. Recoveries, recaptures, and resightings were all very different events, but the type of recovery was not always clearly written on many of the cards. Early on in the program, duplicate band numbers were issued to both bird and bat banders simultaneously, and there were banding records where duplicate bands were applied to individual bats. All of these file-management and reporting errors severely compromised information gathered on recoveries of banded bats. Another problem with recoveries and recaptures was that they were very low. For the large numbers of bats banded from 1932 to 1972, numbers of recaptures and recoveries were not substantial enough to allow for the precise estimation of life history parameters of interest such as survival or population size, except in a few already published cases and for the Townsend's big-eared bat analysis in Part 3 of this report.

Recommendations for the Bat Banding Program Files, Future Bat Marking, and a Bat Marking Clearinghouse

(1) Bat Banding Program Files

This report is an effort to satisfy the need for a comprehensive review and critical evaluation of the BBP and its associated files. The moratorium on bat banding of 1973 specifically stated (Appendix 3): "A detailed evaluation will be made of the files of the bat-banding program. The purposes of this review are to determine the value and relevance of the biological data that have been accumulated in the files, and to study the feasibility of automated techniques for the storage and retrieval of data if the program is to continue." While the BBP files may contain valuable historical information on banded bats previously unpublished, this information is buried in more than 90 drawers of index cards. The main purpose for computerizing the BBP files would be to make them accessible for analyses, specifically analyses involving the use of mark-recapture techniques for *post hoc* estimation of important biological parameters in bats. However, the value of the mark-recapture information in the files is doubtful due to the incomplete files, invalid recoveries and reporting errors, band injuries, band loss, inconsistent type of bands applied to bats, and low recovery and recapture rates described in detail throughout this report.

The dataset on banding of Townsend's big-eared bats by Senger likely represents the most complete and well-maintained unpublished datasets in the BBP files. Although this current analysis is important and provides the only CJS-based estimates of survival for the Townsend's big-eared bat that I am aware of, the quality of the remaining BBP files and the value of results do not justify the computerizing of all the banding records to conduct *post hoc* survival analysis for other species and locations. This dataset was very clean, records were maintained well by both the bat bander and the BBP filing process, recaptures were high, and there appeared to be no band loss from chewing or natural wear and tear. It is doubtful that any other datasets in the BBP files that have not already been published exist of the quality of Senger's dataset. If a few overlooked and unpublished datasets exist in the BBP files that are of similar quality to Senger's, these would require a lot of time digging through the files to find. If such high-quality banding records were found, they could be entered into the prototype USGS Bat Banding Database created for this report. These banding records could then be further summarized to create encounter histories for mark-recapture analyses such as those conducted for this report. However, care would need to be exercised when interpreting the results from these analyses because recoveries were often very low, studies were not often well designed, and bands often directly injured many bats, thereby invalidating some of the assumptions underlying mark-recapture models.

The computerization of the entire BBP files would be a huge undertaking. I estimate that one full-time data entry person could enter one drawer in a day. If the drawer contained many recoveries, it might take 2 days due to the fact many of the cards might have recovery data on the back as well as the front of the cards. It could conceivably take someone 100 working days, or approximately 5–6 months, to enter all existing information contained on cards generated by the BBP. After the files were entered into a database, further time would be required to check for inevitable data-entry errors in transferring the information from the cards into the database. This would add a few weeks to the computerization process. Based on the results of this report, the finished database would primarily serve as an interesting historical resource for summarizing unpublished records of banded bats by location and geographic areas, by species, age, and sex, and by general patterns of recoveries (dead recoveries, recaptures, resightings, and returns). Many bat banders did not publish their studies, and the only record of their work exists in the BBP files or in their own personal records scattered around the country. The only other potential use for this database would be to provide a baseline for any future attempts to create and manage a clearinghouse for bat-marking information for the United States.

I conclude that computerizing the BBP files in their entirety would provide no additional information of value to our current knowledge of population biology of bats. This conclusion is based on the numerous problems with the quality of the data in the BBP files, the time and effort it would take to enter the files, and the limited amount of information we would obtain from further analyses and summaries. However, the potential still exists for bands to be recovered that were applied during the BBP, so it is important to point out that reports of band recoveries are still of interest to researchers (Peurach, 2004). The USGS will continue to receive information on bands issued by the BBP and will provide information from the BBP files upon request. Although the likelihood of band recoveries issued by the BBP diminishes with every passing year, recoveries of banded bats have been reported and published into this century (Navo and others, 2002). I encourage the sharing of information regarding bat banding data and recoveries to: Biological

Survey Unit, USGS, Patuxent Wildlife Research Center, Smithsonian Institution, P.O. Box 37012, National Museum of Natural History, Room 378 MRC 111, Washington, D.C. 20013–7012.

(2) Future Bat Marking

Based on this report and other studies examining the effects of forearm bands on bats (Baker and others, 2001; Dietz and others, 2006), I recommend that marking of bats with standard metal or plastic split-ring forearm bands not be considered for mark-recapture studies, or any study involving marked bats, unless the information sought and the potential for obtaining unbiased estimates from that information vastly outweighs the potential negative effects to the bats. Also, the inferences made from banded bats can never be extrapolated to the population level simply because banded and unbanded bats will likely not have the same fates, a major assumption of mark-recapture theory.

A critical look at the effects of different banding and marking techniques is needed (O'Shea and Bogan, 2003). At the workshop on monitoring trends in bat populations in the United States and Territories, convened in Estes Park, Colorado, in 1999, two of the working groups that formed had suggestions on marking bats. As the "Working Group A" stated, "all current marking techniques present special concerns and these concerns should be addressed with the advice of a biologist experienced with the species before a marking program is begun." The following methods of marking individual bats were elucidated by the working group: (1) Wing bands are known to be seriously injurious to some species, and some species will not tolerate bands; (2) necklaces can be snagged on projections; (3) radios are short-lived, expensive, and, due to the weight and antenna, may cause behavioral changes; (4) fur dyes, wing punches, and freeze branding could potentially be toxic, short-lived, and have unknown long-term effects on bat health; (5) for passive integrated transponders (PIT tags), there is a need to focus bat emergence from roosts through relatively small spaces and there is an unknown long-term effect of PIT tags on survival; and (6) microtaggants are short-lived with unknown toxicity. Microtaggants are injectible, laminated, plastic particles containing layers of fluorescent and magnetic material, previously not used as a bat marking technique. The working group suggested more research was needed for a few of these marking techniques such as dyes, PIT tags, and microtaggants. Double-marking techniques could be incorporated into these studies to investigate their different rates of tag loss. "Working Group C" suggested that one or more studies could be designed to investigate the specific effects of different marking techniques, such as PIT tags compared to bands or other techniques, and how they affect traits critical to bat population dynamics such as survival and reproduction. These studies could first be conducted on abundant and common species not sensitive to disturbance (for example, little brown bats or big brown bats). For example, a 5-year project investigating big brown bats and rabies in an urban setting used PIT tags to successfully answer questions related to sampling techniques and survival of the bats (Neubaum and others, 2005; Wimsatt and others, 2005, Ellison and others, 2006), but more research is needed to investigate the effects of this marking technique on bats and other information that can be extracted using PIT-tagged bats.

Future mark-recapture studies of bats should be limited to well-designed projects, with populations of bats that are not sensitive to disturbance by manipulation and handling, and where the long-term effects of the marking method can be monitored. These studies should be designed with the greatest care and be very specific about the questions to be asked. Issues of importance in the design of these studies include defining and selecting a representative sample of the population of interest, defining and selecting a valid and representative sampling frame, and selecting random locations within this sampling frame. The study design should attempt to minimize the negative effects of capturing and marking individuals, determine age and sex accurately, conduct marking and capturing during a time period where movement, migration, or mortality is negligible, and mark bats during as short a period as possible relative to the intervals between sampling. The problem of tag loss should be minimized because it biases the resulting parameter estimates and violates a key assumption of mark-recapture analyses. Capture probabilities should be as high as possible to obtain the most precise estimates of the parameters as possible. Precision of estimates also tends to increase as the number of sampling occasions increases. For a more thorough examination of study design issues and mark-recapture techniques and analyses, see Burnham and others (1987), Williams and others (2002), and Amstrup and others (2005).

(3) Develop Web-Based Clearinghouse on Marked Bats

I suggest developing a Web-based clearinghouse on marked bats. There has been talk at scientific meetings and in issues of *Bat Research News* that there should be a new clearinghouse formed for tracking bat marking activities around the country. For instance, in 1983 *Bat Research News* "Letters to the Editor," T.W. French writes about finding a banded bat in Mt. Aeolus cave in Bennington County, Vermont. The bat had an unidentified band on it with flanged ends and the number 093. It was not a USFWS band. He further asked if there was any clearinghouse for the coordination of current banding activities. Both Griffin and Hitchcock had previously banded at this cave, but the band was not one of theirs. A request for information on banded Indiana bats and gray myotis was solicited in a 1999 issue of *Bat Research News* (Kurta, 1999). In this request, Kurta pointed out that the majority of bands applied to bats currently do not readily identify the bander and consequently, information on movements and longevity of bats is potentially lost. He requested information on bands applied to Indiana bats and gray myotis that was obtained from sources other than USFWS bat bands. The Northeast Bat Working Group was assembling a list of banders and information concerning the bands that were being used. Finally, at the workshop on sampling problems and monitoring trends in U.S. bat populations in 1999, scientists in one of the working groups specifically discussed the issue of "optimizing information obtained from marked bats" (O'Shea and Bogan, 2003).

Based on the recommendations of the working group at the bat-monitoring workshop, I recommend that this Web-based clearinghouse include information and links to studies that involve the individual marking of bats. The Web site could serve as a centralized resource, providing information and references on proper bat-marking techniques as a means for exchange of marking information. The Web site could also include a list of contacts, a bibliography of related references, and a review of mark-recapture practice and theory as they pertain to bats. It could provide a forum for the exchange of information on methods, marking techniques, recent advances in statistical techniques, and other issues related to mark-recapture studies. Another potential function of this Web site could be to serve as a repository for metadata on marking projects.

Conclusions

This report summarizes the U.S. Government's Bat Banding Program (BBP) from 1932 to 1972. Currently, the files for the program are maintained by the USGS, Patuxent Wildlife Research Center, Biological Survey Unit at the Smithsonian Institution, National Museum of Natural History, Washington, D.C. More than 2 million bat bands were issued by the BBP from 1932 to 1972, of which approximately 1.5 million were applied to 36 species of bats by scientists, their students, and colleagues in many locations in North America including the United States, Canada, Mexico, and Central America. Many interesting facts about basic bat biology were discovered by the application of these bands, including homing behavior, return rates, distances bats are capable of traveling, longevity, seasonal migrations, hibernation ecology, mortality and survival rates, and reproductive behavior. However, the BBP was plagued with numerous problems during its entire tenure. The three main problems were issues with the USFWS bands, disturbance to bat populations from research and banding activities, and problems with the BBP files and recoveries. Bands not only caused direct injuries to bats but were frequently chewed by the bats so that the numbers would become illegible. The quality of the bands varied throughout the program with some bands made from such a soft aluminum alloy, they would not last beyond a single season after banding. There was no consistency in the type of band used on bats due to constant experimentation with different types of bands in an attempt to find a less injurious, longer lasting means of individually marking bats. Disturbance by banding at bat roosts was implicated in bat population declines in 22 North American species because banding activities would often occur during critical periods such as hibernation or periods of recruitment. Finally, the BBP files were incomplete and not well organized, with many instances of reporting errors, which compromised information based on recoveries and recaptures. Overall recoveries and recaptures of banded bats were low. The retrospective analysis of a select dataset in the BBP files in this report provided relatively precise estimates of survival for wintering Townsend's big-eared bats; however, this dataset was unique due to its well-maintained and complete state and because there were high recapture rates over the course of banding. It is doubtful that any other unpublished datasets of the same quality exist buried in the BBP files for further analyses.

Based on the findings from this report, I make the following three recommendations: (1) the BBP files should not be computerized in their entirety because the resulting analyses would provide no additional information of value to our current knowledge of population biology of bats; (2) marking bats with standard metal or split-ring forearm bands should not be considered for mark-recapture studies unless the information sought and the potential for obtaining unbiased estimates from that information vastly outweighs the potential negative effects to the bats; and (3) a Web-based clearinghouse should be developed to serve as a centralized resource on bat-marking methods, mark-recapture techniques, and for the exchange of information on marked bats.

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Appendixes

Appendix 1. An alphabetical list of 107 researchers requesting U.S. Fish and Wildlife Service bat bands in the Bat Banding Program files with city and State or country of residence from 1965 to 1971. The year last bat bands were issued is in parentheses, if known.

1. Atallah, Sana – Shiraz, Iran
2. Baker, Robert J. – Lubbock, Tex. (1970)
3. Baker, W. Wilson – Tallahassee, Fla. (1969)
4. Bateman, Gary C. – Flagstaff, Ariz. (1969)
5. Bechtel, William A. – Portland, Maine (1969)
6. Beck, Albert J. – Davis, Calif.
7. Bergner, Roland –Harrisburg, Pa.
8. Birney, Elmer C. – Minneapolis, Minn. (1971)
9. Black, Hal L. –Albuquerque, N. Mex. (1970)
10. Bordner, Dorothy L. – State College, Pa.
11. Bowles, John B. – Pella, Iowa (1971)
12. Bradshaw, C. – Tucson, Ariz.
13. Brenner, F.J. – Greenville, Pa. (1969)
14. Bridge, D. – Hyattsville, Md.
15. Brown, Larry N. – Tampa, Fla. (1971)
16. Brown, Patricia C.–Los Angeles, Calif. (1971)
17. Carpenter, Charles C. – Norman, Okla. (1968)
18. Clark, Patricia E. – Los Angeles, Calif.
19. Cockrum, E. Lendell – Tucson, Ariz.*
20. Cope, James B. – Richmond, Ind. (1968)*
21. Cross, Stephen P. – Ashland, Oreg.
22. Davis, Wayne H. – Lexington, Ky.*
23. Davis, Russell – Tucson, Ariz.
24. DeBlase, Anthony F. – Ill. (1971)
25. Delpieitro, Horacio – Argentina
26. Dobie, James L. – Birmingham, Ala.
27. Easterla, David – Maryville, Mo. (1971)
28. Farney, John P. – Lawrence, Kans. (1971)
29. Fenton, M. Brock – Toronto, Canada (1967)
30. Findley, James S. – Albuquerque, N. Mex.
31. Glass, Bryan P. – Stillwater, Okla. (1968)*
32. Goehring, Harry H. – St. Cloud, Minn.*
33. Golden, Barry – Macon, Ga. (1970)
34. Gould, Edwin – Baltimore, Md. (1971)
35. Greenhall, Arthur M.– Mexico (1970)
36. Greer, J. K. – Norman, Okla.
37. Grigsby, Everett M.–Tahlequah, Okla. (1969)
38. Gunier, Wilbur J. – Higginsville, Mo. (1970)
39. Guzman, Arturo J. – Mexico (1971)
40. Hall, John S. – Reading, Pa. (1971)
41. Handley, Charles, Jr. – Washington, D.C.
42. Harvey, Michael J. – Memphis, Tenn.
43. Hatch, Jeremy J. – New York, N.Y.
44. Hayward, Bruce J. – Silver City, N. Mex. (1971)
45. Heltsley, James R. – Clarksville, Tenn.
46. Herrel, Clyde F. – Kerrville, Tex.
47. Hinesley, Landis L. – Rantoul, Ill. (1971)
48. Hitchcock, Harold B.–Lewiston, Maine (1971)*
49. Hoffmeister, Donald F. – Urbana, Ill. (1970)
50. Hudson, Jack W. – Ithaca, N.Y.
54. Keefer, Lucy A. – Temple, Pa. (1970)
55. Keefer, Scott D. – Carbondale, Ill. (1970)
56. Keiser, E.D., Jr. – Baton Rouge, La.
57. Kerr, Larry R. – Macomb, Ill. (1970)
58. Kerridge, David C. – Ottawa, Ontario
59. Kirkpatrick, Ralph D.– Jonesboro, Ind. (1971)
60. Koestner, Joseph – Dayton, Ohio (1971)
61. Kranbahl, Michael S.–Cincinnati, Ohio (1968)
62. Kuns, Merle – Argentina (1969)
63. Kunz, Thomas H. – Lawrence, Kans. (1969)
64. Laidlaw, George – Ontario (1971)
65. LaVal, Richard–College Station, Tex. (1969)
66. Layne, James N. – Lake Placid, Fla.
67. Leitner, Philip– St. Mary's College, Calif. (1971)
68. Lewis, James C. – Nashville, Tenn.
69. Linhart, Samuel – Washington, D.C.
70. Lord, Rexford D. – Argentina (1971)
71. Ludwig, James–Mackinaw Islands, Mich. (1968)
72. Martin, Robert L. – Rapid City, S. Dak. (1970)
73. McLean, Robert G. – Lawrenceville, Ga. (1970)
74. Meester, J. – Pretoria, South Africa
75. Myers, Richard F. – Kansas City, Mo. (1970)
76. New, John G. – Oneonta, N.Y.
77. Northcott, Tom H. – Ontario (1968)
78. Pagels, John F. – New Orleans, La. (1968)
79. Parmalee, Paul, W. – Springfield, Ill.
80. Perry, Alfred E. – College Place, Wash.
81. Sealander, John A. – Fayetteville, Ark. (1969)
82. Senger, Clyde M. – Bellingham, Wash. (1967)
83. Sinor, Allen – Daly City, Calif. (1968)
84. Smith, Donald A. – Ontario (1970)
85. Smith, Elizabeth – Smithville, Ohio (1969)*
86. Smith, Hugh C. – Edmonton, Alberta
87. Smith, James Dale – Fullerton, Calif. (1969)
88. Snyder, Dana P. – Amherst, Mass.
89. Spenrath, Curtis A. – College Station, Tex. (1970)
90. Spencer, Dwight L. – Emporia, Kans.
91. Stanley, William C. – Kansas City, Mo.
92. Stone, Robert C. – Houghton, Mich.
93. Studier, Eugene H. – Las Vegas, N. Mex.
94. Suttkus, Royal D. – Belle Chasse, La. (1970)
95. Svendsen, Gerald E. – La Crosse, Wis. (1968)
96. Tamsitt, J. R. – San Juan, P.R.
97. Thomas, Maurice E. – Cali, Colombia (1970)
98. Tinkle, Donald W. – Lubbock, Tex.
99. Turner, Larry – Portland, Oreg.
100. Tuttle, Merlin D. – Lawrence, Kans. (1970)
101. Tyson, Edwin L. – Canal Zone, Panama (1969)
102. Walley, Harlan D. – DeKalb, Ill. (1968)
103. Watkins, Larry C. – Maryville, Mo. (1971)

51. Humphrey, Stephen R.–Stillwater, Okla. (1968)	104. Wilcox, Michael J. – Toronto, Ontario
52. Jones, Clyde – Washington, D.C. (1971)	105. Wilson, Don E. – Costa Rica (1971)
53. Jones, J. Knox, Jr. – Lawrence, Kans. (1968)	106. Wilson, Nixon – Cedar Falls, Iowa
	107. Wolf, James L. – Birmingham, Ala.

*Banders active in 1932–51 (Mohr, 1952).

Appendix 2. The policy on bat banding and bat conservation issued by the Mammal Section of the Bird and Mammal Laboratories, Bureau of Sport Fisheries and Wildlife. The adoption of this policy was announced at the 1972 Symposium on Bat Research in San Diego, Calif., and later ratified by the American Society of Mammalogists in June 1973. Reproduced by permission of the U.S. Geological Survey, Patuxent Wildlife Research Center at the Smithsonian Institution, National Museum of Natural History, Washington, D.C.

Policy on Bat Banding and Bat Conservation

In view of the obvious needs for conservation of bats in North America, the Bureau of Sport Fisheries and Wildlife has adopted a new policy with regard to this important matter. The three major points of the Bureau Policy are as follows:

1. Because it has been demonstrated that bat banding and corresponding activities are a major cause of disturbance to bat colonies, a moratorium has been placed on the issuing of bat bands either to new bat banders or for new banding projects. The current supplies of bat bands will be issued to investigators for use in the completion of ongoing, pertinent projects that do not involve species of bats with greatly reduced populations.
2. A detailed evaluation will be made of the files of the bat-banding program. The purposes of this review are to determine the value and relevance of the biological data that have been accumulated in the files, and to study the feasibility of automated techniques for the storage and retrieval of data if the program is to continue.
3. Appropriate steps will be taken to explore the possibility of developing an international treaty for the protection of North American bats. Every effort will be made to establish a conservation program based on what is best for bat populations, with detailed knowledge of bat biology utilized as the basis for decisions. Necessary actions will be implemented as soon as possible with regard to this part of the program.

Appendix 3. Published sources containing information on bats banded with U.S. Fish and Wildlife Service bat bands during the Bat Banding Program (BBP) from 1932 to 1972. Included are the source, purpose of banding if stated, date and season of banding, location, species, number banded, number of recoveries if reported, and comments. Number of recoveries includes dead recoveries (both foreign and local), returns (from homing experiments), recaptures (or also called "repeats"), or resightings. The number banded and number of recoveries is further divided into adult males (AM), adult females (AF), juvenile males (JM), and juvenile females (JF) if the source provided this information.

Source	Purpose of banding	Date, season	Location	Species	Number banded total (AM:AF:JM:JF)	Number of recoveries (AM:AF:JM:JF)	Comments
Albright (1959)	Longevity, movements, population size	1958, Summer	Oregon Caves National Monument, Oreg., USA	COTO EPFU MYCA MYEV MYLU/VO MYTH MYYU	12 (9:3) 2 (1:1) 9 (8:1) 213 (185:28) 68 (58:10) 29 (26:3) 40 (29:11)	117	The numbers recovered were not reported by species. There was also a problem of misidentification of two species: a few of the MYLU were later identified to MYVO.
Baker (1965)	Movements, population size	1963–1964, Multiple	3 caves and 1 concrete tunnel, Georgia, USA	EPFU LABO MYAU MYGR MYLU MYSE MYSO PESU NYHU	100 (26:74) 81 (42:39) 2 (2:0) 90 (79:11) 3 (2:1) 96 (72:24) 2 (1:1) 983 (730:253) 526 (58:468)	16 (6:10) 16 (15:1) 3 (2:1) 1 (1:0) 167 (117:50) 255 (6:249)	
Banfield (1948)	Longevity, Recovery reports	1948, Winter	Lafleche Cave, Gatineau County, Quebec, Canada	EPFU	16	10	Two of the recoveries reported were males banded by H.B. Hitchcock on November 25, 1939. Authors did not report sex of remaining 8 recovered bats or who originally banded them.

Barbour (1950)	Recovery reports	1937, Spring	Bat Cave, Carter County, Ky., USA	MYLU MYSO	2,000	46	The numbers originally banded and recovered were not reported by species. Barbour reported recoveries for bats originally banded by Welter and Sollberger (1939).
Barbour and Davis (1974)	Natural history	1963, Summer	Mammoth Cave National Park, Ky., USA	Multiple species	>12,000	Not specified	Not clear in text how many bats of which species were originally banded. A few summaries of banding were embedded in the individual species accounts, but it was not easily summarized.
Barbour and others (1966)	Homing	1965, Fall	Bat Cave, Carter County, Ky., USA	MYSO	140	14	This study blinded bats to see if vision was necessary for homing.
Bateman and Vaughan (1974)	Dispersal, population size	1969, Summer	Cavern system, Sinaloa, Mexico	PTPA PTPE PTDA	1,475 (47:1,428) 70 (26:44) 84 (25:59)	17	The numbers recovered were not reported by species.
Beer (1955)	Movements, survival	1940–1953, Winter	Multiple locations, Minnesota and Wisconsin, USA	EPFU	3,871	251	Used life table analyses for survival estimation. Twenty-five of the bats were recovered away from the original banding site.
Bowles (1981)	Natural history	1980–1981, Summer	Multiple sites, Iowa, USA	EPFU LANO LABO LACI MYLU MYSE MYSO NYHU PESU	245 55 132 32 44 70 61 41 6	Not specified	

Bowles (1983)	Longevity, recovery reports	1982, Summer	State Fish Hatchery, Delaware County, Iowa, USA	MYLU		1	This recovered bat was originally banded by R.F. Myers 23 years earlier at the same site.
Brack (1983)	Natural history	1980–1981, Summer	Multiple sites, Indiana, USA	LABO LACI NYHU	79 32 41	None reported	Also used plastic split-ring bands (A.C. Hughes) on other species not reported here.
Brenner (1968)	Population size, reproduction	1965–1967, Summers	2 human-made structures in Ohio and Pennsylvania, USA	EPFU	175 (Ohio) 775 (Pa.)	Not specified	
Brenner (1974)	Hibernation ecology, movements, population size	1965–1970, Winters	Laurel Caverns, Fayette County, Pa., USA	MYLU	2,914	Not specified	Population size was estimated, but number of recaptured bats was not reported.
Burnett and Kunz (1982)	Age estimation, growth rates	1978, Summer	Attic, Middlesex County, Mass., USA	EPFU	118	None reported	Short-term growth rates were determined.
Clark (1984) Clark and others (1987)	Natural history	1980–1983, Summer	Multiple sites, Iowa, USA	EPFU LANO LABO LACI MYLU MYSE MYSO NYHU PESU	362 63 165 42 339 108 67 42 11	Not clear	Used a combination of USFWS bands and plastic split-rings (A.C. Hughes), but it was not clear which species was banded with which type of band.

Cockrum (1952)	Longevity, recovery reports	1941, Winter	Morrison Cave, Monroe County, Ill., USA	PESU	57 (46:11)	3	The 3 recoveries reported were males of unknown age. The assumption was made that USFWS bands were used because of the date of the publication and band issue information in the BBP files.
Cockrum (1956)	Homing, longevity, movements	1954, Summer	Colossal Cave, Pima County, Ariz., USA	COTO MYVE	54 68 (12:56)	3 ~2	It is unclear exactly how many of the MYVE banded were recovered, but they were all females.
Cockrum (1969)	Migration, recovery reports	1952–1967, Summer	Eagle Creek Cave, Ariz.	TABR	88,176 (10,852:77,324)	1,210 (159:1,051)	Recoveries were only reported for these 3 sites. Total number of TABR banded in Ariz. was 104,781, 3,251 for N. Mex., and 54,754 for Mexico.
			Silver Creek Bridge, Ariz.	TABR	1,371 (215:1,154)	254 (66:188)	
			Carbo, Sonora, Mexico	TABR	40,794 (19,155:21,639)	1,027 (447:580)	
Cockrum and Ordway (1959)	Natural history	1955, Summer	Southwestern Research Station, Portal, Ariz.	EPFU	1 (1:0)	1	Male EPFU recovered that same season.
				COTO	56 (8:22:12:14)	3 (0:3:0:0)	COTO adult females recovered that same season.
				TABR	630 (353:277)	0	
Cockrum and others (1996)	Movements, population size	1959–1964, Multiple	Multiple sites, Arizona, USA	MACA ANPA COTO EPFU IDPH LACI MYCA MYCI MYTH	1,667 (709:958) 370 (146:224) 1,661 (376:1,285) 499 (127:372) 145 (18:127) 2 (1:1) 122 (41:81) 7 (3:4) 1,162 (321:741)	464 (189:186) 30 (4:26) 222 (24:198) 27 (9:18) 53 (1:52) 0 1 (0:1) 0 17 (4:13)	Recoveries were reported in publication as “local” or “foreign.”

				MYVE MYVO MYYU PAHE TABR	1,342 (740:602) 240 (87:153) 199 (38:161) 1,080 (300:780) 3,335 (1,656:1,679)	91 (68:23) 11 (10:9) 9 (5:4) 43 (3:40) 0	
Cohen (1944)	Homing	1941, Fall	Building, Prince George's County, Md., USA	EPFU	3 (1:2)	1 (1:0)	
Constantine (1967)	Natural history, population size	1956–1958, Summer	Carlsbad Caverns, N. Mex., USA	TABR	28,900 (11,132:17,768)	333 (92:241)	The total number banded and subsequently recaptured was calculated from tables 1, 5, 6, and Appendix tables 3–6.
Cope and Hendricks (1970)	Population size	1969, Summer	7 buildings, Indiana, USA	MYLU	11,139	None reported	The assumption was made that USFWS bands were used because of the date of the publication and band issue information in the BBP files.
Cope and Humphrey (1967)	Homing	1964, Summer	Attic in building, Montgomery County, Ind., USA	NYHU	210	36	The total number banded included juvenile bats of unspecified sex.
Cope and Humphrey (1977)	Swarming behavior	1961–1965, Fall	Wyandotte Cave, Crawford County, Ind., USA Wind Cave, Breckinridge County, Ky., USA	MYSO	4,278	None reported	The total number of bats banded by sex and location is not clear in text.
Cope and Mumford (1955)	Movements, sex ratios	1951–1954, Winter	23 caves in south-central Indiana, USA	EPFU LANO LABO MYAU	411 2 11 29	None reported	This is a preliminary report of bats banded in south-central Indiana.

				MYLU MYSE MYSO PESU	3,756 17 1,400 534		
Cope and others (1958)	Homing	1954–1957, Summer	Tunnelton, Lawrence County, Ind., USA	MYLU	1,774 (456:1,196:122)	372	Returns of homing bats were reported as a percentage. Twenty-one percent returned 34 days later to the original banding location. Juvenile bats were of unknown sex.
Cope and others (1961b)	Homing	1961, Summer	6 buildings, Indiana, USA 2 buildings, Brookeville, Ind., USA	EPFU MYLU	167 (20:147) 40 (0:40)	69-80 (0:69-80) 32-36 (0:32-36)	Returns were reported as a range of values because the authors used a radioactive labeling technique to estimate number of returns.
Cope and others (1974)	Natural history	1972–1973, Summer	Nolands Fork River, Wayne County, Ind., USA	EPFU LANO LABO LACI MYLU MYSE MYSO	106 2 28 8 15 3 31 (25:2:4)	None reported	Age and sex were only reported for MYSO.
Cross (1965)	Movements	1961–1962, Summer	Sabino Canyon, Ariz., USA	PAHE	25	7	The assumption was made that USFWS bands were used because of the date of the publication and band issue information in the BBP files.

Davis, R. (1966); Davis, R., and Cockrum (1962)	Homing	1957–1961, Multiple	Multiple sites, Arizona and New Mexico., USA	MACA ANPA COTO EPFU MYKE MYTH MYVE TABR	31 (9:22) 719 (278:441) 38 (1:37) 212 (37:175) 1 (1:0) 159 (41:118) 96 (28:68) 1,465 (391:1,074)	2 (1:1) 210 (47:163) 1 (1:0) 55 (0:55) 1 (1:0) 39 (0:39) 1 (1:0) 300 (90:210)	
Davis, R. (1969)	Growth rates	1966–1968, Summer	Multiple bridges, Arizona, USA	ANPA	545 (0:0:285:260)	~230	It was unclear how many were recaptured. Number of recoveries reported was summed from table 1.
Davis, R. and Cockrum (1963)	Homing	1960–1961, Summer	Night roost, Tucson, Ariz., USA	ANPA	112 (112:0)	6 (6:0)	
			Bridge, Nogales, Ariz., USA	EPFU	9	4	
			Bridge, Graham County, Ariz., USA	MYVE	45	2	
			Multiple sites, Arizona, USA	TABR	124	17	
Davis, R.B., and others (1962)	Natural history, survival	1957, Summer	Multiple buildings and caves, Texas, USA	TABR	21,140	177	
Davis, W.H. (1957, 1959, 1966b)	Sex ratios, survival	1952–1965, Multiple	Greenville Saltpeter Cave, W. Va., USA	PESU	5,708 (4,303:1,405)	714 (616:98)	Number of recoveries reported was for 1953–56 (Davis, 1957). Recoveries were not reported in Davis (1966), but author banded bats through 1965 at both of these caves.
			Thorn Mountain Cave, W. Va., USA		5,454 (4,383:1,044)	594 (531:63)	

Davis, W.H. (1964b)	Swarming behavior	1963, Fall	Dixon Cave, Ky., USA	Multiple species	12,000	None reported	This was a very short note in the National Speleological Society's Bulletin and did not give details on number of bats banded or recoveries.
Davis, W.H. (1969b, 1970)	Natural history	1966, Summer	Arizona, USA	LACI	300	2(2:0)	
Davis, W.H. and Barbour (1970a)	Homing	1966, Fall	Bat Cave, Carter County, Ky., USA	MYSO	270 (270:0)	117 (117:0)	Half of the bats banded were blinded for the homing study.
Davis, W.H. and Barbour (1970b)	Natural history	1968, Summer	Building, Conejos, Colo., USA	MYVO	45 (0:45)	0	
Davis W.H. and Hardin (1967)	Homing	1966, Summer	Willow Creek, Catron County, N. Mex., USA	LANO	3 (3:0)	1 (1:0)	The assumption was made that USFWS bands were used because of the date of the publication and band issue information in the BBP files.
Davis, W.H. and Hitchcock (1964)	Hibernation ecology, sex ratios	1961–1962, Winter	Mine, Essex County, N.Y., USA	EPFU	115 (81:34)	None reported	The assumption was made that USFWS bands were used because of the date of the publication and band issue information in the BBP files.
			Mine, Ulster County, N.Y., USA	MYLU	3,977 (2,503:1,474)	None reported	

Davis, W.H. and Hitchcock (1965)	Homing, migration, natural history	1960–1963, Multiple	Connecticut, USA Maine, USA Massachusetts, USA New Hampshire, USA New Jersey, USA New York, USA Ontario, Canada Quebec, Canada Rhode Island, USA Vermont, USA	MYLU	3,769 1,477 3,232 2,988 6 17,725 793 6 1,344 42,476	Not clear	Anecdotal recaptures and recoveries reported in text, but not summarized. The assumption was made that USFWS bands were used because of the date of the publication and band issue information in the BBP files.
Davis, W.H. and Lidicker (1955)	Unclear	1954, Winter	Mine, Grant County, Wis., USA	MYLU	274		It was unclear why these bats were banded. This was a note about a specimen of MYSO collected from the same site so it was not specifically about the banding.
Davis, W.H. and others (1965)	Natural history	1963–1964, Summer	Buildings, Kentucky, USA	MYLU	3,363 (595:2,768)	25 (9:14:2:0)	
Davis, W.H. and others (1968)	Behavior	1963–1965, Summer	Buildings, Kentucky, USA	EPFU	147 (0:58:89)	7 (1:2:0:4)	

DeBlase and others (1965)	Recovery reports	1964, Spring	Wind Cave, Breckinridge County, Ky., USA	MYLU MYSO PESU	~4,000 ~200 ?	776 46 3	Authors reported recoveries of dead bats that were originally banded by J.B. Cope. Actual number of bats originally banded was not specified in text.
Duke and others (1979)	Longevity	1978, Summer	Heiser Spring, Coconino County, Ariz.	MYCA	?	1 (0:1)	This was a 15-yr (minimum age) longevity record for this species. Bat was originally banded by T.A. Gustafson in 1963 and total number banded was not specified in text.
Dunnigan and Fitch (1967)	Homing, movements, population size	1963–1966, Multiple	Mines and caves, Barber and Comanche Counties, Kans., USA	MYVE	>2,000	Unclear	Numbers of recoveries and recaptures were unclear. There were scattered accounts of recoveries throughout the text that were difficult to summarize.
Eads and others (1955)	Migration	1954, Summer	Bracken Cave, Comal County, Tex., USA	TABR MYVE	3,814 486	None reported.	
			Ney Cave, Medina County, Tex., USA	TABR	700		

Easterla (1972; 1973)	Homing, migration, movements, population size	1967–1971, Multiple	Big Bend National Park, Tex., USA	LENI ANPA COTO EPFU EUMA LACI MYCA MYTH MYVE MYVO MYYU PAHE EUPE MOME NYFE NYMA TABR	568 (217:473) 797 (324:473) 363 (86:277) 50 (33:17) 13 (4:9) 9 (1:8) 13 (9:4) 316 (99:217) 39 (24:15) 2 (2:0) 292 (83:209) 199 (88:111) 52 (12:40) 24 (2:22) 44 (7:37) 284 (10:274) 484 (394:85)	1 24 8 0 0 0 0 50 1 0 22 0 0 0 0 0 0	
Easterla and Watkins (1970)	Natural history	1965–1969, Summer	Buildings, Missouri and Iowa, USA	NYHU	2,109 (297:1,812)	5	Numbers of recoveries were dead recoveries. Authors stated that returns and repeat captures were "fairly common," but they did not specify this in text.
Elder and Gunier (1978; 1981)	Movements, sex ratios	1968–1975, Winter	Marvel Cave, Stone County, Mo., USA	MYGR	18,768 (7,863:10,905)	2,166 (615:1,551)	
Fenton (1966)	Natural history	1965, Winter	Two caves, Jefferson County, N.Y., USA	MYSO	503 (260:243)	Not reported	

Folk (1940)	Hibernation ecology, movements	1937-–1938, Winter	Indian Oven Cave, N.Y., USA	MYLU	332	116	
Gifford and Griffin (1960)	Homing	1957, Fall	Mine, Chester, Mass., USA	MYLU	365	79	The number of recoveries represented by returns from a homing experiment.
Glass (1958; 1959; 1982)	Migration, movements, recovery reports	1952–1968, Summer	Multiple caves, Oklahoma, USA	TABR	170,000	Not enumerated	Author displayed recoveries in the figures, but did not enumerate the totals by sex and age.
Goehring (1954; 1958; 1972)	Natural history, survival	1951–1971, Winter	Storm sewer, St. Cloud, Minn., USA	EPFU	960 (645:315)	1,046 (698:348)	
Griffin (1934)	Natural history, early banding techniques	1932–1933, Summer	Building, Cape Cod, Mass., USA	MYLU	161	3	Bands were placed on the bats' tibias.
Griffin (1936)	Natural history, early banding techniques	1932–1936, Multiple	Multiple sites, Cape Cod, Mass. and caves in Vt., USA	EPFU MYLE MYLU MYSE MYSO PESU	28 2 1,562 26 1,329 41	700	Authors did not summarize returns or recaptures by species and location.

Griffin (1940a; 1940b; 1945)	Homing, migration, natural history	1932–1939, Multiple	Multiple sites, Connecticut, Massachusetts, New Hampshire, New York, Vermont, USA	EPFU MYLE MYLU MYSE MYSO PESU	165 11 7,651 1,144 2,370 398	2,000	Author did not summarize returns and recaptures by species, sex, age, and location. Griffin (1945) was a summary paper on migratory travels of banded bats (13,000 total). He focused on 15 “foreign” returns of MYLU and MYSO that were banded in the previous publications.
Griffin and Hitchcock (1965)	Longevity, recovery report	1960, Spring	Cave, East Dorset, Vt., USA	MYLU		1 (0:1)	Authors did not state how many bats were originally banded at this location. This was a 24-yr longevity record for MYLU.
Grigsby (1980)	Movements, natural history	1968–1978, Multiple	6 caves, Missouri and Oklahoma, USA	MYGR	6,858 (2,111:4,747)	894 (320:574)	
Gunier (1970) and Gunier and Elder (1971)	Homing, natural history	1967, Summer	Building, Moniteau County, Mo., USA	MYGR	437 (110:327)	107 (23:84)	Recoveries reported were from a homing experiment within one summer season.
Hall (1962)	Natural history	1956–1960, Multiple	Multiple sites, Illinois, Indiana, and Kentucky, USA	MYSO	11,557	~100	It was unclear how many of each sex were originally banded. It was also unclear how many were recovered or recaptured after initial banding.

Hall and Brenner (1968)	Natural history	1964–1965, Summer	Aitkin Cave, Mifflin County, Pa., USA	EPFU	7		It was unclear how many were recovered or recaptured.
				MYLE	3		
				MYLU	1,060 (713:347)	~130	
				MYSE	173 (140:33)		
				PESU	17		
Hall and Davis (1958)	Homing	1955–1956, Spring	Blackball Mine, LaSalle County, Ill., USA	EPFU	9	2 (2:0)	It was not clear how many of each sex were originally banded.
Hall and Wilson (1966)	Movements	1958–1961, Multiple	Winter, Coach-James Cave, Edmonson County, Ky., USA	MYGR	3,072 (1,558:1,514)	12 (1:11)	
			Summer, 7 caves, Illinois and Kentucky, USA	MYGR	1,622 (485:1,137)	153 (64:89)	
Hall and others (1957)	Longevity, recovery reports	1955–1956, Fall	Cave, Vermont, USA	MYLU	744	1 (0:1)	This study reported on two recoveries. It was unclear how many MYSE were originally banded by Griffin in 1936–1937.
			Mine, Chester, Mass., USA	MYSE	?	1	
Hassell (1963)	Homing	1962, Fall	Bat Cave, Carter County, Ky., USA	MYSO	700 (281:419)	119	The number of recaptured bats was displayed as a percentage (table II).
Hassell (1967)	Movements	1964–1965, Winter	Bat Cave, Carter County, Ky., USA	EPFU	34	Unclear	Bats were watched throughout the winter to document intra-cave movements, but total number of “recaptures” were not reported in text. Used plastic “parakeet” bands on some of the bats in addition to USFWS bat bands.
				MYLU	86		
				PESU	180		

Hassell and Harvey (1965)	Homing	1963, Fall	Bat Cave, Carter County, Ky., USA	MYSO	1,572 (0:1,572)	641 (0:641)	
Hays and Bingman (1964)	Recovery reports	1961, Fall	Storm sewer, Pittsburg, Kans., USA	MYGR		3 (0:3)	Recoveries reported were from bats originally banded by R.F. Myers in 1959. Author did not report total number originally banded by Myers.
Hays and others (1983)	Natural history, recovery reports	Unknown	Storm sewer, Pittsburg, Kans., USA	MYGR	2,408 (1,042:1,362) 698	170	Bands were originally applied by T.H. Kunz (2,408) and E. Grigsby (698).
Hayward (1961; 1970)	Natural history	1953–1960, Multiple	Multiple locations, Arizona, USA	MYVE	13,000	1,140	
Herreid and others (1960)	Survival	1956–1959, Unknown	Unknown	TABR	252	573	Authors recaptured bats to assess injuries due to bat banding using bird bands and newly designed “bat bands.” Individual banded bats were recaptured multiple times.
Hitchcock (1940; 1950; 1955; 1965); Keen and Hitchcock (1980); Hitchcock and others (1984)	Early banding techniques, movements, natural history, survival	1939–1962, Summer	Multiple locations, Ontario and Quebec, Canada	EPFU MYLU	206 (57:149) 1,947 (183:1,764)	Not reported Not reported	
		1939–1962, Winter	Multiple locations, Ontario and Quebec, Canada	EPFU MYLE MYLU MYSE PESU	648 (446:202) 626 (305:321) 4,622 (3,233:862) 362 (281:81) 131 (107:24)	518 (418:100) 173 (103:70) 2,601 (2,365:236) 27 (27:0) 18 (16:2)	

Hitchcock and Reynolds (1942)	Homing	1939–1941, Summer	2 summer colonies, Middesex County, Ontario, Canada	MYLU	443 (0:308:24:111)	359 (0:248:0:111)	
Howell and Little (1924)	Natural history	1921, Summer	Garage, Los Angeles County, Calif., USA	EPFU	5 (0:5)	2 (0:2)	Authors did not use USFWS bat bands, but this reference was included because it was a classic banding reference.
Humphrey (1969)	Natural history	1968, Summer	Unknown roost, Oklahoma, USA	COTO	80	0	All bats banded appeared to vacate the roost after being handled.
			Sculpture Cave, Okla., USA		8	0	
Humphrey (1971) and Humphrey and Cope (1976)	Hibernation ecology, migration, movements, population size, reproduction, sex ratios, survival, swarming behavior	1952–1969, Multiple	Multiple locations, Indiana and Kentucky, USA	MYLU	71,706	14,336	Recoveries reported were a combination of recaptures, recoveries, and resightings. The 14,336 reported here was the number of recaptures of 10,760 individuals. Numbers of the other two types of recoveries were not easily found in the dissertation.
Humphrey and Cope (1963)	Movements	1959–1963, Summer	Colony, Boone County, Ind., USA	MYLU	1,710	313	The 313 reported recoveries were recaptured at the same location. Forty-seven were recaptured at other locations.

Humphrey and Cope (1968)	Migration	1959–1962, Multiple	Buildings, Indiana, USA	NYHU		3 (0:1:2:0)	Authors did not specify how many bats were originally banded.
Humphrey and Cope (1970)	Population size, sex ratios, survival	1964–1965, Summer	2 nursery colonies, buildings, Indiana, USA	NYHU	526 (0:208:0:210)	195 (0:74:0:51)	108 individuals of the 526 banded were not aged (and 70 of the reported recaptures were from these 108).
Humphrey and Cope (1977)	Survival	1952–1976, Multiple	Multiple caves, Indiana and Kentucky, USA	MYSO	9,059	5,023	Recaptures reported could be from some bats captured more than one time.
Humphrey and Kunz (1976)	Hibernation ecology, movements, population size, reproduction, sex ratios, survival	1967–1974, Multiple	Multiple caves, Oklahoma, USA	COTO	~800	~66	It was unclear in the text exactly how many bats of each sex and age were banded.
Humphrey and others (1977)	Natural history	1974–1975, Summer	Tree roost, Indiana, USA	MYSO	20-30		Female adults and young were banded, but authors were not clear on exactly how many were banded over the two summers. A combination of USFWS bands and plastic colored bands (A.C. Hughes) were used. Number of recaptures was not reported.

Jones (1964)	Natural history	1962, Summer	Mine tunnel, Catron County, N. Mex., USA	MYVO MYTH	39 (0:39) 21 (0:21)		No purpose for the banding was given in text and no recaptures or recoveries were reported. The assumption was made that USFWS bands were used because of the date of the publication and band issue information in the BBP files.
Jones and Pagels (1968)	Natural history	1965–1966, Multiple	Buildings, Plaquemines Parish, La., USA	PESU	190 (85:105)	113 (46:67)	
Jones and others (1967)	Distributions, natural history	<1967, Multiple	Multiple locations, Kansas, USA	EPFU MYGR MYLU MYSE MYVE PESU TABR	9 309 (239:70) 400 1,000 1 400 14		Occasionally, recoveries were reported in text, but only those related to distributional records. No complete summary was available on total numbers recaptured or recovered.
Kunz (1971a; 1973)	Growth rates, population size, reproduction, sex ratios	1968–1971, Multiple	Multiple buildings, mines, and caves, Kansas and Oklahoma, USA	MYVE	14,158 (7,417:6,741)	446 (203:243)	Recoveries reported were from table 32 in the publication, which displayed the relative movement from selected nurseries to winter roosts. Actual numbers of recoveries and recaptures were not clearly stated in text.
Kunz (1971b)	Natural history, reproduction	1967–1969, Summer	Des Moines River, multiple sites, Boone County, Iowa, USA	EPFU LANO LABO LACI MYLU MYSE	242 (109:66:39:28) 51 (4:23:12:13) 124 (15:52:31:28) 26 (0:7:16:3) 27 (8:14:4:1) 65 (17:40:2:6)		Number of recoveries was not reported in text.

Kunz (1974)	Reproduction, growth rates, survival	1968–1970, Summer	Building, Dorrance, Russell County, Kans., USA	EPFU	107 (0:0:46:61)	51 (0:0:21:30)	Author banded neonates for estimating growth rates.
Kunz and Anthony (1982)	Age estimation, growth rates	1978, Summer	2 buildings, Grafton and Hillsborough Counties, N.H. , USA	MYLU	121	64	All of the bats banded were nonvolant juveniles of unspecified sex. Nineteen individuals were recaptured twice, 28 were recaptured three times, 15 were recaptured four times, and two were recaptured five times during a single summer season.
Landrum (1971)	Longevity, movements, natural history, recovery report	1970–1971, Summer	Multiple maternity colonies, Delaware, Grant, Hamilton, and Madison Counties, Ind., USA	EPFU	602 (82:422:34:53)	Unclear	Seven of the 602 were banded by others in previous studies (6 and 12-yr minimum ages were determined). Original banders were R. Kirkpatrick and J.B. Cope.
LaVal (1973a)	Natural history	1965–1966, Summer	3 buildings, Clinton, La., USA	TABR	957	319	Number banded and recaptured not separated out by sex and age
LaVal (1973b)	Natural history, population size	1968–1970, Summer	McKittrick Canyon, Guadalupe Mountains National Park, Culberson County, Tex., USA	Multiple species			It was unclear how many were banded versus how many were collected. Authors state, "all bats not prepared as specimens were banded and released."
Leffler and others (1979)	Homing	1961–1971, Winter	Hibernia Mine, Morris County, N.J., USA	MYLU	>10,000	101 175?	The 101 recoveries were reported by the public. It was not clear exactly how many were recovered by the authors.

Mills (1971)	Natural history	1969–1970, Summer	3 caves, Adams County, Ohio, USA	EPFU LABO MYLU MYSE PESU	30 9 135 578 (391:207) 92	 18 	Authors reported recaptures for MYSE only and did not report number recaptured by sex.
Mills and others (1975)	Age estimation, population size, survival	1969–1972, Multiple	81 summer maternity colonies and 2 winter hibernacula, Ohio and 3 winter hibernacula, Indiana, USA	EPFU	10,761	Unclear	Banded individuals were recaptured in subsequent years, but number by sex and age not reported in text.
Milstead and Tinkle (1959)	Natural history	1956–1959, Multiple	Multiple sites, Texas, USA	COTO TABR	61 188	Not reported	The number banded were specified by sex and age.
Mohr (1933a)	Early banding techniques, movements	1932, Summer	Cave, near Reading, Pa., USA	MYLU MYSE MYSO PESU	“several dozen” Unknown Unknown Unknown	Unclear	“about half a dozen marked bats returned to the cave, little brown bats and pipistrelles making the flight.” “Fingerling tags used on ears.”
Mohr (1933b; 1939)	Early banding techniques	1931–1933, Multiple	Multiple caves, Berks County, Pa., USA	MYLE MYLU MYSE PESU	54 72 43 11	12 13 9 5	Author was unclear how many bats were banded with “fingerling” fish tags on the ears or banded on the tibia with USFWS bands.
Mohr (1934)	Natural history, early banding techniques	1931–1933, Multiple	Multiple caves, Pennsylvania, USA	MYLE	~29	~1	Author was unclear on how many bats were banded with USFWS bird bands on the tibia and how many were marked with “fingerling” fish tags on the ears.

Mohr (1939)	Early banding techniques, natural history, recovery reports	1933–1939, Winter	South Penn Railroad Tunnels, Pa., USA	EPFU	65			
				MYLU	364		17	
				MYSO	19			
				PESU	315		13	
Mohr (1942a; 1942b)	Early banding techniques, natural history, recovery reports	1932–1935, Summer	Building, Kempton, Berks County, Pa., USA	MYLU	500		"many returned"	Author was unclear on how much overlap this paper had with previous publications (Mohr, 1933a; 1933b; 1933c; 1939)
		1933–1942, Winter	Multiple sites, Pennsylvania, USA	MYLE	198		21	
		1938–1942, Winter	Woodward Cave, Pa., USA	MYLU	236		118	
		1939–1942, Winter	Durham mine, Pa., USA	MYLU	1,312		Unclear	
Mohr (1945)	Sex ratios	1942–1945, Winter	Maitland Cave, Mifflin County, Pa., USA	EPFU	292		52	

Mumford (1958)	Hibernation ecology, population size, sex ratios	1954–1955, Winter	Cave, Lawrence County, Ind., USA	EPFU	107(59:48)	40(21:19)	Of the 40 reported recapture, some were recaptured more than once. Additionally, two recoveries were reported by the public to the BBP.
Myers (1964a)	Movements, natural history	1954–1962, Multiple	Multiple locations, Illinois and Missouri, USA	MYGR	2,527	235	Author was unclear on how many of each species was banded and how many were recovered, recaptured, or returned. For MYSO, 3,448 of the 3,608 reported returned one or more times to the original banding site and 160 were dead recoveries.
				MYLU	4,427		
				MYSO	21,321 (10,055:11,266)	3,608	
Myers (1964b)	Recovery reports	1959, Winter	2 caves, Laclede County, Mo., USA	MYGR	2 (2:0)	2 (2:0)	These recoveries were reported from Kans. by H.A. Hayes.
Orr (1954)	Natural history	1947–1952, Multiple	Multiple locations, San Luis Obispo and Kern Counties, Calif., USA	ANPA	20	8	Author was unclear on how many were banded. Number reported here was a minimum estimate. Bats were maintained in captivity before being banded and released.
Pagels and Jones (1974)	Growth rates, sex ratios	1967–1969, Multiple	Building, New Orleans, La., USA	TABR	374 (207:167) all juveniles	Not reported	
Patterson (1961) and Tinkle and Patterson (1965)	Behavior, hibernation ecology	1957–1963, Winter	Panther, Walkup, and Sinkhole Caves, Tex., USA	MYVE	11,620	~5,000 recaptures	Recoveries reported were recaptured bats. Authors did not specify the number of bats banded and recovered by sex and age. They stated there were 0.39 males to females in total captures (and recaptures).

Pearson and others (1952)	Natural history, reproduction	1948–1951, Multiple	Multiple locations, California, USA	COTO	>1,500		Authors did not report actual numbers of recaptures or returns, but reported a 75 to 80 percent return rate for adults and 54 percent return rate for juveniles.
Perry (1965); Perry and Rogers (1964)	Age estimation	1962–1964, Summer	5 caves, Oklahoma, USA	TABR	49,800 juveniles	Not reported	Sex of juvenile bats banded was not reported.
Phillips (1966)	Hibernation ecology, homing, population size, sex ratios, survival	1962–1964, Multiple	Mine and storm sewer, Kansas, USA	EPFU	515(304:211)	50	The number of recoveries reported was dead recoveries (not reported by sex or age).
				MYLU	7	Not reported	
				PESU	7	Not reported	
Reynolds (1941)	Homing	1940, Summer	Building, Middlesex County, Ontario, Canada	EPFU	98(0:35:36:27)	11(0:9:2:0)	
Rice (1957)	Behavior, natural history, survival	1953–1955, Multiple	Multiple sites, Florida	MYAU	2,751	706	The recoveries reported were a combination of returns, repeat captures, and dead recoveries (not reported by sex).
Rogers (1972)	Natural history, sex ratios	1962–1967, Summer	Multiple caves, Oklahoma and Texas, USA	TABR	110,000 "neonatal young"	Not reported	A.E. Perry and G. Beckett banded young in an earlier publication (Perry 1965). Author unclear on how many were banded in this study compared to Perry and Beckett's earlier work.

Rysgaard (1942)	Natural history	1940–1941, Winter	Multiple caves, Minnesota, USA	EPFU MYLU MYSE PESU	900 2 6 10	Not reported	
Schramm (1957)	Homing	1956, Summer	Unknown, Des Moines County, Iowa, USA	MYLU	34	2	The assumption was made that USFWS bands were used because of the date of the publication and band issue information in the BBP files.
Short (1961); Short and others (1960)	Movements, reproduction	1955–1958, Multiple	Multiple caves and buildings, Texas, USA	TABR	36,000	176	Authors also reported on “foreign” recoveries from previous banding efforts (B. Villa, R., D.G. Constantine, B.P. Glass, and R.B. Eads).
Sidner (1997)	Survival, longevity	1980–1995, Summer	3 bridge roosts, Cochise County, Arizona, USA	ANPA EPFU	1,702 2,231	11,342 13,849	Number of recoveries reported is number of recaptures and could be multiple captures of the same individual. Bats were initially banded with USFWS bands, but later in the study they were banded with aluminum bands from Gey Band and Tag Company and (or) Lambournes, Ltd. Author unclear on number of bats banded with USFWS bands.
Smith (1957)	Sex ratios	1950–1957, Multiple	Multiple roosts, northern Ohio, USA	MYLU	3,768 (39:2,213:641:875)	Unclear	Author reported there were 3 “returns” from 178 males banded at Dulaney’s Cave, but no recaptures or recoveries were reported elsewhere.

Smith and Goodpaster (1963)	Growth rates	1963, Summer	Maternity colony, Mason, Ohio, USA	EPFU	16 (0:0:16:0)	Not reported	
Smith and Hale (1953)	Homing	1952, Unknown	Building, Wilmington, Ohio, USA	MYLU	77 (35:42)	2 (0:2)	
Sommers and others (1993)	Longevity, recovery reports	1992, Winter	Iron mine, Essex County, N.Y.	MYLU	9,379 (7,842:1,537)	7 (7:0)	The recoveries reported were resightings of bats originally banded in 1961–62 by Davis and Hitchcock. These resighted bats were therefore at least 31 and 30 years old.
Spenrath and LaVal (1974)	Natural history	1969–1970, Fall	Building, College Station, Tex., USA	TABR	1,063	Unclear	Table 1 in article gave percentages of recaptured bats by sex and number of times they were recaptured, but the actual number of individuals recaptured in total was unclear.
Stevenson and Tuttle (1981); Tuttle (1976b; 1979); Tuttle and Stevenson (1977)	Movements, migration, survival	1960–1971, Summer	50 caves in Alabama, Forida., and Tennessee, USA	MYGR	40,182	6,486 71	Of the 40,182 bats banded, 21,505 were adults, 12,829 were juveniles, and 5,848 were yearlings and individuals of unknown age. Recoveries reported were only for three major caves. Total number of recoveries was not clearly stated. Seventy-one of the recoveries were submitted by the public. Tuttle (1979) stated that approximately 23,000 banded gray myotis had been recaptured during his studies.

Stones and Branick (1969)	Homing	1967, Fall	Mine, Baraga County, Mich., USA	MYLU MYSE	55 25	11 3	Bats were divided into four experimental groups and one control group. Experimental groups were blinded, blindfolded, deafened, or deafened and blinded.
Tibbetts (1956)	Homing	1956, Fall	Hole in cliff, Justiceburg, Tex., USA	EPFU TABR	8 7	2 1	The assumption was made that USFWS bands were used because of the date of the publication and band issue information in the BBP files.
Tinkle and Milstead (1960)	Population size, sex ratios	1958–1959, Winter	3 caves, Texas, USA	MYVE	3,288	~1,325	Number of recoveries were recaptures and resightings displayed as a percentage in tables IV-VI. Therefore, total number recovered was estimated from these percentages.
Trapido and Crowe (1946)	Early banding techniques	<1946, Unknown	“Northeastern” caves, Unknown, USA	Multiple species	~5,000	Not reported	This publication described a banding technique. Authors banded with W.A. Wimsatt.
Turner (1974)	Natural history	1968, Summer	Multiple caves, South Dakota, USA	MYCI MYVO EPFU	35 70 6 (5:1)	Not reported	Reported on 9 returns of COTO originally banded by the National Park Service.
Tuttle (1975; 1976a)	Growth rates, survival	1969–1970, Spring	6 caves, Tennessee River drainage system, Alabama and Tennessee, USA	MYGR	5,626	Unclear	Bats banded were volant juveniles. Authors reported recoveries as a percentage in fig. 5 (Tuttle 1976a).

Twente (1955a; 1955b)	Hibernation ecology, movements, natural history	1952–1953, Winter	Multiple caves, Kansas and Oklahoma, USA	ANPA COTO EPFU MYVE	8 155 60 911	Not reported 51 Unclear 151	
Villa and Cockrum (1962)	Migration	1952–1962, Multiple	Multiple sites, Arizona and New Mexico, USA, and Mexico	TABR	~32,000	60	The 60 recovered were "foreign" recoveries. Authors were unclear on how many total bats were recovered, recaptured, or resighted.
Walley (1970)	Movements, recovery reports	1961–1968, Multiple	Blackball Mine, LaSalle County, Ill., USA	MYLU Multiple species	7,873 4,127	38	For the 4,127 multiple species banded, author was unclear on how many of each species was banded.
Walley and Jarvis (1971a,b)	Longevity	1971, Winter	Blackball Mine, LaSalle County, Ill., USA	PESU		1 (1:0)	This bat was originally banded in February 1957 so longevity record for this individual was at least 14.8 years.
Welter and Sollberger (1939)	Longevity, migration, natural history	1937, Spring	Bat Cave, Carter County, Ky., USA	MYLU MYSO	2,000	70	Total banded and total resightings not reported by species.
Wilson and Findley (1972)	Homing	>1972, Unknown	Barro Colo. Island, Panama Canal Zone, Panama	MYNI	134		The number of returns was reported as a percentage in table 1 and was based on the distance bats were released from original banding location.

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