Fascinating Life Sciences

Burton K. Lim · M. Brock Fenton
R. Mark Brigham · Shahroukh Mistry
Allen Kurta · Erin H. Gillam
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50 Years of Bat Research

Foundations and New Frontiers

NASBR
North American
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Bat Research

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Foreword

I have attended over a dozen North American Society for Bat Research meetings, often with the support of the UK's Bat Conservation Trust, to whom I reported on the state of bat conservation in North America. I always considered NASBR to be the best of the growing number of bat meetings. The highlight was always the student presentations when dozens of well-rehearsed and well-turned-out graduates were keen to impress those faculty who they might approach for admission to a master's or doctoral program. And NASBR has always shown how valued they are, with a growing number of student awards. When my budgets allowed, I brought my own students, including those from overseas, and the NASBR meeting was one of the highlights of their training.

NASBR provided me with an opportunity to meet many of the leaders in bat biology, particularly my guru Bill Wimsatt (Albuquerque, 1978), in the days when I was still a reproductive biologist. And much later, Don Griffin (Burlington, 2002), whose *Listening in the Dark* book had got me into bats when I was an undergraduate in Cambridge in the 1960s. Don had taken a sabbatical in Cambridge, and his legacy was a question on an examination paper "How do bats echolocate?" which I chose for my weekly essay.

There were also memorable personalities like Karl Koopman who listened to every presentation and whose frequent questions were invariably prefaced by "It seems to me . . ." Art Greenhall and his artist and writer wife who sat dutifully through every session.

I greatly valued the academic stimulation and camaraderie of NASBR meetings, and I am grateful to those who kept the show on the road—Roy Horst, Brock Fenton, Kunwar Bhatnagar, Tom and Margaret Griffiths, as well as Emily Davis who provided me with an exclusive range of bat ties that were the envy of my UK colleagues.

I only ever had one criticism and that could be reduced to semantics—over the use of the word "banquet" which in the UK means a sumptuous feast with wine. We learned various tricks often involving brown paper bags to overcome the drought!

It has been a great pleasure to witness this informal series of annual meetings mature and evolve into a fully constituted scientific society, and I wish it continued success.

Centre for Ecology and Conservation
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Paul A. Racey

Preface

As the North American Society for Bat Research enters our second half-century of existence, we reflect on our origins from an informal gathering to one of the largest scientific organizations dedicated to the study of the only flying mammals. We have experienced much change during this time and know that our society is resourceful to meet the challenges going into our next 50 years. The annual meeting of NASBR has steadily grown from its beginning under the banner of Symposium on Bat Research in the Southwest in 1970 at Tucson, Arizona, with 2 days and 26 talks. There was no dedicated student session, but 14 of 38 listed authors were students (37%). The 42 registrants were from the USA and Mexico. Canadians first made it to the next meeting in Albuquerque, New Mexico, which prompted a rebranding in 1972 at San Diego as the North American Symposium on Bat Research.

For the first quarter century, Roy Horst did yeoman's service as the Program Director, organizing the meeting each year with a local host. But as the society grew and changed, NASBR became a formal scientific society with the adoption of a constitution and by-laws and establishment of a Board of Directors in 1999 at the meeting in Madison, Wisconsin. At the 2009 meeting in Portland, Oregon, the current name of North American Society for Bat Research was formally adopted.

The group has grown! During the five decades of NASBR meetings, there has been an almost tenfold increase in registrants and papers. In 2019 in Kalamazoo, Michigan, there were 3 days of concurrent sessions featuring 133 oral presentations and two sessions with 76 posters that were attended by 380 participants from 9 countries. With inclusion of co-authors, 27 countries were represented from all the main continents. Students represented 38% of the registrants, similar to the percentage of authors during the first meeting.

For this publication on "50 Years of Bat Research: Foundations and New Frontiers", we solicited contributions from NASBR members and collaborators abroad to survey a breadth of topics on bat biology. We encouraged co-authorship by researchers with different levels of experience, including students, to give broad insights into the areas of study. These review papers typically include a historical perspective of the subject matter based on presentations at earlier NASBR meetings, progressing to the current state of knowledge, and a prospectus for the future.

The 21 contributions are grouped into 9 general themes. Although some chapters could have been placed into more than one theme, we have arranged them in a similar format to the oral presentation sessions at our annual symposia. Some themes of research in bat biology have changed over the years, whereas others have persisted. For example, a paper on bat acoustic systems was presented at the first meeting by Jim Simmons who is an author of the chapter in this publication on the effects of noise on the biosonar of bats. Echolocation remains one of the primary areas of study in chiropterology with many presentations at NASBR that continue to incorporate acoustic data. Systematics and taxonomy have always been areas of research for our society, but the methods of analysis have evolved from karyotypes to DNA sequences.

As the final edits of this book are being completed in December 2020, we are in the midst of a coronavirus pandemic with >72 million infections and almost 1,620,00 deaths worldwide. It has forced a change in our daily routines including social distancing, virtual meetings, and working at home. At this point, we do not know the effect and impact it will have on bat research other than there will be a new normal, especially for fieldwork. But as research themes have changed over time, virology and molecular biology will surely see a surge of interest to understand better the asymptomatic high viral load of bats.

Furthermore, this global pandemic has delayed our 50th anniversary meeting planned for Tempe, Arizona, in October 2020 to next year. Not the most auspicious start to the second half-century of NASBR, but we have grown in size and adopted a new administrative structure during the first 50 years so we are confident in the continued success of our society.

This special publication of the golden anniversary of NASBR is dedicated to Dr. Thomas H. Kunz, a founding member who passed away on April 13, 2020, due to complications from COVID-19. Tom was presented with the Gerrit S. Miller Jr. Award in 1984, our most prestigious honor in recognition of his outstanding service and contribution to the biology of bats. He hosted our 25th symposium at his university in Boston in 1995, which was held jointly with the International Bat Research Conference. In 1999, Tom was elected to a two-year term on the inaugural Board of Directors of NASBR. Life Membership in our society was bestowed in 2013. But more importantly, Tom was a mentor, colleague, and friend to many of us. We established the Kunz Award in 2018 to recognize an early to mid-career bat researcher who exemplifies many of the qualities of Tom's legacy in research, conservation, mentorship, public education, and international collaborations. This award is to be presented for the first time during the 50th anniversary meeting in Tempe, Arizona, in 2021.

NASBR 50th book editors

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Regina, SK, Canada	R. Mark Brigham
Chico, CA, USA	Shahroukh Mistry
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Fargo, ND, USA	Erin H. Gillam
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Part I
History

R. Mark Brigham

Given that this volume commemorates the first 50 years of meetings of the North America Society for Bat Research, it is intuitive that the first theme of the book is retrospective. The first chapter in this section is an historical perspective of the society with a general history of NASBR written by Gary Kwiecinski and Roy Horst, who served as our current and first program directors, respectively. They bring a thoughtful perspective on where NASBR has come from and why. They trace the 10-fold growth in participants at the annual meeting, the formalization of a governing board, a host of awards, the long-held emphasis on supporting students, the growth in the number of females that are attracted to the meeting and how we support the local community.

The other paper grouped in this section by Fred Frick, Amy Russell, and Erin Gillam reviews the contribution of women to our society and the development of diversity, equity, and inclusivity in NASBR. The highly positive tone of this chapter succeeds in showing how the members of NASBR have worked hard on these issues while at the same time providing us with clear incentive and rationale for why we have to do more and to do better. Survey data of society members also suggest that while much has been accomplished, the task will never be complete.

It will be fascinating to see what the next 50 years brings and how the nature and outlook of the society change. These chapters set the stage for that and will hopefully make NASBR members very proud of where we have come from but anxious to roll up our sleeves and continue the hard work to get even better.

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Chapter 1
NASBR Origins 1970–2020: From an Informal Gathering to a Scientific Society

Gary G. Kwiecinski and G. Roy Horst

Abstract The annual meetings of the North American Society for Bat Research (NASBR) have served as a prominent worldwide forum for the presentation of, and discussion about, research and conservation on bats. NASBR was founded in 1970 as an informal meeting at which individuals with a special interest in bat research could share, discuss, and develop ideas. Before 1999, the sole purpose was to hold an annual meeting for the dissemination of recent findings about bats. In 1999, NASBR became a formal society governed by a Board of Directors, with a constitution and by-laws. Since its inception, the society has grown from a regional meeting to an international scientific organization. This chapter summarizes the primary changes that have occurred along the way and highlights some of the major events over the past half century.

Keywords NASBR · North American Society for Bat Research · North American Symposium on Bat Research · History

The North American Society for Bat Research (NASBR) was founded on November 27, 1970 when the first meeting was held in Tucson, Arizona. The guiding principle for NASBR is reflected in its Mission Statement: "The North American Society for Bat Research promotes the study and conservation of bats by facilitating communication and collaboration among scientists, educators, and the general public." In the 50 years since its inception, the society has held a meeting each year except 1985, when it chose to avoid a conflict with the International Bat Research Conference (IBRC) held in Aberdeen, Scotland. Although most attendees reside in North America, every year the society welcomes participants from all parts of the world.

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The idea for a symposium dedicated to the biology of bats was born out of conversations between colleagues attending the annual meetings of the American Society of Mammalogists (ASM) in the late 1960s. In June 1970, at the ASM meeting in College Station, TX, James Findley, Terry Vaughn, and Roy Horst enjoyed a coffee break together and shared their continuing concerns that on many occasions two presentations about bats were offered at the same time, causing one to miss a presentation. They realized, with a crowded program, such conflict was inevitable, and Horst suggested that those with a special interest in bats might get together at some convenient time and place for an informal meeting. They decided to focus on convening colleagues from the southwestern region of the United States at an easy-to-reach venue.

Horst volunteered to assemble a list of bat biologists and invited them to a short meeting at the University of Arizona (UA) in Tucson over the American Thanksgiving weekend. Phillip Krutzsch, from the Department of Anatomy at UA, agreed to serve as host, provided that Horst did the work of organizing the event, which was called the Symposium on Bat Research in the Southwest. A Friday session was held at UA and a Saturday session at the Arizona-Sonora Desert Museum. In attendance were 42 scientists who presented 26 research reports. At the conclusion of the meeting all agreed that it had been a productive exercise and were enthusiastic about gathering again.

In the following year, James Findley invited the group to meet in Albuquerque at the University of New Mexico, also over Thanksgiving. Horst again agreed to take care of the correspondence and organize the program, and thus, the Second Southwestern Symposium on Bat Research was scheduled. With increasing interest across the United States, Canada, and Mexico, subsequent meetings were called the North American Symposium on Bat Research. For the first 25 years, Horst was the Program Director (PD) and worked with a Local Host (LH) to organize the conference. In 1999 at Madison, Wisconsin, NASBR adopted a constitution and by-laws with an elected Board of Directors who oversee the PD and LH in their planning of the annual meeting, but only the PD and Board Chair can sign contracts on behalf of NASBR.

1.1 The When, Who, and Where of NASBR

Initially, all symposia were held in the southwestern United States, and the first eastern meeting was NASBR 7 in Florida. Subsequently, the meetings were geographically distributed based on local host availability and various attempts to rotate the meetings regionally. The first five symposia occurred during the United States Thanksgiving break in November. Beginning with NASBR 6, October became the most frequent time, with several exceptions. The preferred and most frequent time, by popular acclamation, for the meetings has been the third week of October. However, local venue options, costs, and practical opportunities affected selected dates, and the meeting was convened once in September (NASBR 30) and three times in November (NASBR 11, 32, and 39). On four occasions, when joint meetings were conducted with the IBRC, the symposia were in August (NASBR 9 in Tucson, NASBR 25 in Boston, NASBR 37 in Merida, and NASBR 43 in Costa Rica).

Meetings in the United States have occurred in 23 states and Puerto Rico (Table 1.1). Four symposia have been convened in California; three, in Arizona, Texas, and Florida; and two, in Colorado, Illinois, Massachusetts, Nebraska, New Mexico, New York, and Tennessee. Six meetings have been held in Canada (one in Alberta, British Columbia, and Quebec, and three in Ontario), and the seventh will be in Manitoba (2023). Three meetings have been held in Mexico; including Merida 2007 that was plagued by numerous cancellations when hurricane Dean (category 5) crossed the Yucatan Peninsula during the meeting, leaving much uncertainty about how many registrants actually attended.

At a minimum, 67 individuals have served as Local Hosts or co-Local Hosts of NASBR meetings (Table 1.1). Initially, at the concluding business meeting of the symposium, a Local Host or Hosts volunteered for the next year's meeting and the site was selected. This annual pattern continued until 1998, when selection of the Local Host for meetings 3 years in advance was necessitated, primarily by growth of attendance at annual meetings and difficulty in securing a suitable site. Currently, a LH is selected based on submitted bids voted on at the annual business meeting. Of the 67 individuals who have hosted meetings, Rodrigo Medellin has hosted or co-hosted all three meetings in Mexico. Two meetings have been hosted or co-hosted by Judith Eger, Brock Fenton, James Findley, Roy Horst, Trish Freeman, and Gary McCracken.

1.2 Technical Presentations

The first symposium consisted of 26 oral (platform) presentations, as well as two unscheduled reports (Fig. 1.1). A meeting of 2 or 3 days typically allowed for single sessions. The first 20 meetings consisted of 2 days of single technical sessions, except NASBR 10 in St. Louis and NASBR 12 in Ithaca had 3 days of technical sessions, and NASBR 9 in Albuquerque was 5 days of technical sessions since it was a joint meeting with IBRC. All subsequent meetings have consisted of 3 days of technical session. Single sessions were the norm until NASBR 20 when day two featured concurrent sessions. Concurrent sessions occurred again at NASBR 23 in Gainesville and subsequently returned at NASBR 31 in Victoria and for all subsequent meetings, except NASBR 38 in Scranton. When a large number of oral presentations were submitted for NASBR 38, four concurrent sessions were scheduled to keep poster sessions during afternoons, and allowing for symposia, auction, and receptions to occur during the evenings. Later, poster sessions occurred in either late afternoons or evenings to avoid the chaos experienced and displeasure voiced when there were more than two concurrent oral sessions. The NASBR membership

Table 1.1 Summary of location, local hosts, presentations, and attendees for annual meetings of North American Society for Bat Research (NASBR)

Year	NASBR#	Location	Local host	# Oral presentations	# Posters	# Attendees
1970	SWSBR1	Tucson, AZ	Phil Krutzsch	26		42
1971	SWSBR2	Albuquerque, NM	Jim Findley	29		57
1972	NASBR 3	San Diego, CA	Roger Carpenter	49		93
1973	NASBR 4	New Orleans, LA	Al Gardner	41		117
1974	NASBR 5	Lubbock, TX	Dilford Carter	36		89
1975	NASBR 6	Las Vegas, NV	Glen Bradley & Michael O'Farrell	29		76
1976	NASBR 7	Gainesville, FL	Stephen Humphrey	46		109
1977	NASBR 8	Ottawa, ON	Brock Fenton	35		182
1978	NASBR 9 & IBRC 5	Albuquerque, NM	Jim Findley & Don Wilson	102		217
1979	NASBR 10	St. Louis, MO	James Simmons	53		119
1980	NASBR 11	Los Angeles, CA	James Smith & Donald Patten	32		89
1981	NASBR 12	Ithaca, NY	Bill Wimsatt	66		167
1982	NASBR 13	Louisville, KY	Kunwar Bhatnagar	41	8	107
1983	NASBR 14	Fort Collins, CO	Tom O'Shea	20		59
1984	NASBR 15	Rockford, IL	Larry Forman	43		71
1985	No meeting	IBRC 7 in Scotland	To avoid conflict			
1986	NASBR 16	Amherst, MA	Dave Klingener	34	2	94
1987	NASBR 17	Toronto, ON	Judith Eger, Brock Fenton, & James Fullard	41		106
1988	NASBR 18	Calgary, AB	Robert Barclay	56	11	100
1989	NASBR 19	Knoxville, TN	Gary McCracken & Michael Harvey	55	7	137
1990	NASBR 20	Lincoln, NE	Trish Freeman & Hugh Genoways	56	11	159

(continued)

Table 1.1 (continued)

Year	NASBR#	Location	Local host	# Oral presentations	# Posters	# Attendees
1991	NASBR 21	Austin, TX	Merlin Tuttle & Jackie Belwood	75	13	203
1992	NASBR 22	Quebec City, QC	Don Thomas	67	10	193
1993	NASBR 23	Gainesville, FL	John Seyjaget & Frank Bonaccorso	76	20	231
1994	NASBR 24	Ixtapa, Mexico	Bernardo Villa, Hector Arita & Rodrigo Medellin	72	15	174
1995	NASBR 25 & IBRC 10	Boston, MA	Tom Kunz & Roy Horst	287	118	382
1996	NASBR 26	Bloomington, IL	Thomas & Margaret Griffiths	68	23	201
1997	NASBR 27	Tucson, AZ	Virginia Dalton	76	26	269
1998	NASBR 28	Hot Springs, AR	US Forest Service & David Saugey	70	25	231
1999	NASBR 29	Madison, WI	John Kirsch & Deanna Byrnes	77	33	259
2000	NASBR 30	Miami, FL	Ted and Marcia Fleming	84	33	221
2001	NASBR 31	Victoria, BC	Mark Brigham	94	32	281
2002	NASBR 32	Burlington, VT	Roy Horst & Bill Kilpatrick	83	50	263
2003	NASBR 33	Lincoln, NE	Patricia “Trish” Freeman	72	44	247
2004	NASBR 34	Salt Lake City, UT	Michael Herder	93	55	300
2005	NASBR 35	Sacramento, CA	Winston Lancaster	98	53	350
2006	NASBR 36	Wilmington, NC	Mary Kay Clark	101	63	
2007	NASBR 37 & IBRC 14	Merida, MX	Rodrigo Medellin	240[a]	137[a]	
2008	NASBR 38	Scranton, PA	Gary Kwiecinski	113	58	371
2009	NASBR 39	Portland, OR	Jan Zinck & Pat Ormsbee	116	60	
2010	NASBR 40	Denver, CO	Rick Adams	97	56	
2011	NASBR 41	Toronto, ON	Judith Eger & Burton Lim	131	56	322

(continued)

Table 1.1 (continued)

Year	NASBR#	Location	Local host	# Oral presentations	# Posters	# Attendees
2012	NASBR 42	San Juan, PR	Armando Rodriguez-Duran	108	49	242
2013	NASBR 43 & IBRC 16	San Jose, CR	Bernal Rodriguez-Herrara	321	114	639
2014	NASBR 44	Albany, NY	Emily Davis & Mike Warner	138	67	400
2015	NASBR 45	Monterey, CA	Shahroukh Mistry & Dave Johnston	148	78	427
2016	NASBR 46	San Antonio, TX	Rebecca Patterson & Mylea Bayles	121	68	357
2017	NASBR 47	Knoxville, TN	Gary McCracken & Emma Willcox	118	65	357
2018	NASBR 48	Puerto Vallarta, MX	Jorge Ortega & Rodrigo Medellin	131	56	312
2019	NASBR 49	Kalamazoo, MI	Amy Russell & Maarten Vonhof	130	76	380
2021	NASBR 50	Tempe, AZ	Angie MacIntire & Marianne Moore			
2022	NASBR 51 & IBRC	Austin, TX	Tigga Kingston & Liam McGuire			
2023	NASBR 52	Winnipeg, MB	Craig Willis			

No data exists where there are no numbers

[a] Pre-hurricane, before cancellations

remains reluctant to change the meeting length to more than 3 days of technical sessions, except when a joint meeting occurs with IBRC.

Student honors oral presentations have always been valued and priority sessions at NASBR. The first student-only oral session, designated for “Honoraria,” occurred in 1982 (Louisville, NASBR 13). Subsequently, all Student Honoraria oral presentations have been scheduled for day one of the meeting and were single sessions until NASBR 43 in San Jose, Costa Rica (joint meeting with IBRC) when the number of submissions could not be accommodated in a single-session program. All subsequent NASBR meetings have had concurrent Student Honoraria oral presentation sessions.

The first poster session (eight posters) occurred in 1982 (NASBR 13 in Louisville). For the next three meetings there were no poster presentations, until the 1986 meeting (NASBR 16 in Amherst) when two posters were presented. Subsequent to Amherst, poster presentations have been a permanent fixture. They were typically available for viewing throughout the conference but with a specified time for authors to be present. The first Student Honoraria for poster presentations were at NASBR 20 in Lincoln. NASBR 26 in Bloomington was the first meeting with two poster

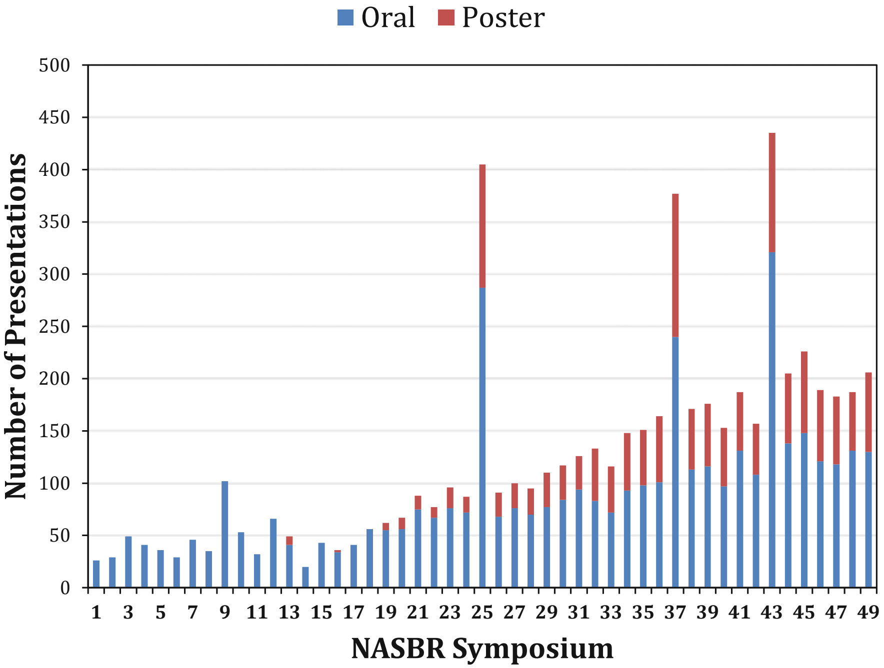

Fig. 1.1 Number of oral and poster presentations for the first 49 years of the North American Society for Bat Research. NASBR symposia 9, 25, 37, and 43 were joint meetings with the International Bat Research Conference (IBRC)

sessions on different days, establishing the current programming format of 1 day for regular posters with day one including Student Honoraria poster presentations.

The society has never evaluated abstracts for acceptance or limited the program to only a select number of presentations. To accommodate as many presenters as possible, the Society has limited the number of presentations (either oral or poster) given by a single person to one, although individuals may be co-authors of an unlimited number of presentations. With continued growth in submissions for presentations and limited space within a 3-day program of two concurrent sessions, the Board recently approved allowing PDs to schedule three concurrent sessions if necessary. However, a current debate among members is whether or not to develop a vetting procedure to limit presentations, such as if submitted abstracts are too speculative and lack data.

Symposia on special topics have occurred within the single and concurrent session formats throughout NASBR's history. In general, these special sessions are requested before the annual meeting (currently at least 1 year in advance). An organized plenary presentation for a specific topic has occurred following student sessions, during concurrent sessions, as a single session following concurrent sessions, and as a special event during the evening. The advent of a plenary session with presentations by the Spallanzani and Bernardo Villa awardees occurred in

Denver (NASBR 40), and the first meeting with an opening plenary session featuring a keynote speaker followed by the Spallanzani and Bernardo Villa awards was San Jose, Costa Rica (NASBR 43) in 2013.

1.3 NASBR Organization and Management

1.3.1 Constitution and By-Law Adoption

Prior to 1999, NASBR prided itself on its informal organization, being an annual gathering of people who met to discuss the latest research on bats. As NASBR grew, it was necessary to adopt a minimal level of organization, particularly for financial reasons, when the annual symposium became of greater interest to governmental taxing agencies. For the first 25 years of NASBR, Roy Horst was the PD who helped select the next meeting venue and he organized the program with the Local Host, a position he executed with aplomb (Horst 1995). Tom and Margaret Griffiths followed Roy as PDs (NASBR 26–35, 1996–2005), and they completed the paperwork and filing for NASBR to become an official, incorporated society in Illinois. They also wrote the Constitution and the By-laws of NASBR (NASBR 1999), based on those of other organizations, including the America Society of Mammalogists and American Association for the Advancement of Science. Tom also had input from an attorney who was a personal friend and who had participated in similar projects in the past. The NASBR Constitution and By-laws were presented and formally approved on October 30, 1999, in Madison (NASBR 29) by unanimous acclamation; in addition, six members were elected to the new board of directors and an impromptu meeting occurred at the very end of the symposium in Madison (Griffiths 1999). The first official Board meeting was held in Miami the following year. At this juncture, NASBR changed from an informal group to a 501(c) (3) not-for-profit (IRS exempt) society on December 18, 2001. One of the important consequences of registering as a not-for-profit organization was that NASBR could now accept monetary donations without tax consequences.

1.3.2 NASBR Officers

The original Constitution identified the officers of NASBR as the PD, the previous year's Local Host, current Local Host, next year's Local Host, and a six-person Board of Directors who are elected by the membership. The directors are the only voting members of the administrative organization of NASBR; all other members are ex officio and advisory, except in the case of a tie vote, in which case the PD may cast a vote.

In Madison, after adoption of the Constitution and By-laws, the first six Board members were elected: Roy Horst and Pat Morton (1-year term), Trish Freeman and

Tom Kunz (2-year term), and Hector Arita and Robert Barclay (3-year term). Staggered terms allowed two new directors to be elected at each subsequent annual meeting. The first Board included ex officio members John Kirsch, 1999 Local Host, Ted Fleming, 2000 Local Host, Mark Brigham, 2001 Local Host, and Tom Griffiths, the PD. At the first Miami Board meeting in 2000, the election of Board Chair and a combined position of Secretary/Treasurer was deferred until the second Board meeting and after the election of the two, new, incoming Board members during the Business meeting. Robert Barclay was elected as the first Chair of the Board, and Trish Freeman was elected as the first Secretary/Treasurer of NASBR.

Since student involvement in the annual Symposium was always desirable and encouraged, a student observer, Dan Riskin, was added to Board meetings to help address issues and concerns of students at the 2002 meeting in Burlington, Vermont. Subsequently, in 2004, the number of student observers was increased to two. The importance and role of students in driving NASBR activities was further recognized in 2008 when the Constitution was amended to change the status of student observers to non-voting Student Board members, elected by students only, to serve a 1-year term, which was subsequently changed to 2-year, staggered terms by amendment in 2011. In 2017, Student Board members were given the same privileges as regular members, including voting rights.

1.3.3 Amendments to the Constitution and By-Laws

The NASBR Constitution and By-laws are evolving documents that represent how the society conducts its business. If the society recognizes a need to update the Constitution and By-laws, they can be changed by amendment. To change the Constitution by amendment, a written petition by any ten members or by a majority of the Board must be presented to membership prior to a members' annual meeting for debate, and acted upon with approval of two-thirds majority of attendees required for adoption. Amendments to the By-laws may be initiated and presented after a majority vote of the Board or by individual members prior to a meeting of NASBR for debate and acted upon at an annual business meeting, requiring two-thirds majority of attendees for approval.

The Constitution was amended in 2003, 2008, 2012, 2015, and 2017, and the By-laws were amended in 2008, 2012, and 2017. A significant change to both documents occurred in 2008 (approved by mail-in ballot in April 2009), when the name of the North American Symposium on Bat Research was officially changed to the North American Society for Bat Research. At this time, the nature of the Board also changed. The original Constitution called for a board of six directors, with two elected each year for 3-year terms. Since it took at least 1 year for directors to get "up to speed" on NASBR issues, their effectiveness became elusive, especially for the Chair of the Board. The high turnover in Board members resulted in a paucity of institutional memory and inefficiency in completing NASBR business. Also, it was sometimes difficult to reach a majority with a six-member board. Thus in 2008, the

Constitution was amended to expand the Board to nine directors and allowed individuals to be re-elected to a second 3-year term, with no director elected beyond the second term without being off the Board for at least 1 year. At this time, the Treasurer was made a non-voting member of the Board by appointment from the Board. The Treasurer was previously a position elected from among the Board members. Another change was that the two elected student observers were made non-voting Student Board members for 1-year terms by adding a new article to the constitution. A major change to the By-laws at this time was the establishment of a new Article allowing the Board to designate committees, with a Board member serving as Chair of such committees. The Chair of a NASBR committee can appoint additional members of the committee, and the Chair of the Board and PD sit as ex officio members of all committees.

In 2011, with Treasurer DeeAnn Reeder's reorganization of the financial records after taking over in 2008, the Board and DeeAnn initiated a change in the official location of NASBR for efficiency purposes from Illinois to Pennsylvania, her home state. The Board accepted the Commonwealth of Pennsylvania Articles of Incorporation for Non-profit Corporation of The North American Society for Bat Research. A further change occurred in 2011 when Student Board member's terms were increased to 2-years and their elections/terms staggered by a year. Subsequently, in 2012, the length of Board member's term was increased from 3 to 5 years to ensure continuity and efficiency of the Board by further increasing longevity and institutional memory.

In 2015, changes to the Constitution and By-laws included allowing voting by electronic means, carrying out business between annual meetings, allowing up to two Local Hosts (ex officio) on the Board, and allowing Associate PDs (ex officio) to be on the Board. In 2017, changes to the Constitution added defined terms for removal of a Board member, and to the By-laws, a new section was added whereby the Board may impose penalties on a NASBR member for violations of the Code of Conduct.

A review of elected directors of the Board since its inception in 1999 revealed primarily Americans: however, at least one Canadian has been on the Board every year except 2010, and at least one Mexican has been on the Board every year until 2018. Past Board Chairs, in chronological order include: Robert Barclay, Betsy Dumont, Maarten Vonhof, Matina Kalcounis-Rueppell, Shahroukh Mistry, Deanna Byrnes, Allen Kurta, and Burton Lim. There have been 26 male and 14 female Board members, with the current Board composed of five females and four males. In 2007, Betsy Dumont as Chair of the Board, established a "Board of Directors Guide to NASBR." to help direct the Board in its duties and responsibilities. In 2015, Allen Kurta created the "Acts of the Board of Directors" to provide a history and reference of Board actions and policies. Since their creation, the Guide and Acts have been updated each year. The Board established in 2019 a mentorship program for each incoming Board member to be paired with an experienced Board member for orientation to the ever-increasing complexities of the duties and responsibilities of the Board.

Policies, acts, and statements adopted by the Board include: Abstract Acceptance Policy, Alcohol Policy, Code of Conduct Policy, Conflict of Interest Policy, Intellectual Property Policy, One Presentation Policy, Online Comment Policy, Role of Science Statement, Inclusion Statement, and establishment of two Ombudspersons that report to the Chair of the Board. Resolutions adopted by the Board and approved by the membership include: Rabies and Bat Bites; White-nose Syndrome in Bats; Bats and Emerging Infectious Diseases; and Bats and Wind-Energy Development. The Board also issued a "Position Statement of the Board of Directors—Bats and Ebola" to counter media reports suggesting bats as the source of Ebola virus outbreaks in West Africa. Standing committees established by the Board include: Finance, Policy and Public Relations, Sponsorship, Nominations, Education and Outreach, Diversity, Equity and Inclusion, Awards, Miller Award, Spallanzani Award, Villa Award, Kunz Recognition Award, and Auction.

1.3.4 Program Directors

The PD, according to the By-laws "…is authorized to produce the annual symposium in conjunction with a Local Host…appoint Associate Program Directors, or other persons to assist in the production of the annual meeting. The Program Director is authorized to enter into contracts on behalf of NASBR…". People who served as PD include Roy Horst (NASBR 1–25, 38–39), Tom Griffiths (NASBR 26–35), Mary Kay Clark (NASBR 36), and Gary Kwiecinski (NASBR 40–50). There was no PD for NASBR 37, a joint meeting with IBRC in Merida, MX, when the LH performed all programming. Associate PDs include Margaret Griffiths (NASBR 26–35), Frank Bonaccorso (NASBR 40–45), Shahroukh Mistry (NASBR 43–50), Luis Víquez-Rodríguez and Riley Bernard (NASBR 46–present), and Emma Wilcox (NASBR 48–present).

While Roy Horst was the first and longest running PD when NASBR was an informal gathering, Tom and Margaret helped marshal many of the formalities to recognize NASBR as an official society. Tom and Margaret Griffiths helped establish an operating budget for the annual meeting and two student award funds (Koopman and Villa), which subsequently grew into six awards by the 35th meeting and ten awards by the 48th meeting. Elizabeth (Dixie) Pierson was instrumental in helping NASBR establish the Bernardo Villa Fund for assisting Latin American students studying in Mexico to attend NASBR. With Pat Morton and Jackie Belwood, Tom and Margaret also helped establish the first Teacher Workshop for local area educators at NASBR 26 (Bloomington).

During the Scranton meeting (NASBR 38), Roy Horst came back to serve as PD for the next 2 years while Gary Kwiecinski (Local Host) and Frank Bonaccorso (former Board member) volunteered to serve as PDs-in-training for the Portland (NASBR 39) meeting, which was the first under the banner of the new name North American Society for Bat Research. Beginning at Denver (NASBR 40), Gary served as PD and Frank as Associate PD.

Prior to the Denver meeting, the registration process and fee collection method established by Tom Griffiths was with a third-party vendor (SkipJack). Since NASBR faced some structural challenges at this time, and another party was administering the NASBR website, a new approach was taken to consolidate NASBR's organizational needs. To this end, Frank Bonaccorso and Gary Kwiecinski recruited, in 2013, an additional Associate Program Director, Shahroukh Mistry (former Board Chair), to oversee revising the registration and website systems. Prior to this, DeeAnn Reeder was recruited (2008) to be NASBR's Treasurer, and with the PDs, Shahroukh and DeeAnn developed an internal on-line registration and fee-collecting system using a commercial platform. At this time, Shahroukh also established a website maintenance system.

Recently, NASBR has developed a more comprehensive and informative program style for the annual meeting including a listing of pre- and post-conference events, a program overview with map of the venue, highlighting major NASBR program sponsors and student award sponsors, plenary speaker biographies, bids for future meeting venues, nominees to the Board of Directors, and a list of participant emails (optional for individuals). In addition, the PDs and the Board of Directors now produce a summer newsletter, *Lasiurus*, to summarize events of the previous and upcoming meetings.

To aid in the transition stemming from the retirement of Frank Bonaccorso as Associate PD in 2015 and the pending retirement of Gary Kwiecinski and Shahroukh Mistry as PDs in 2021, additional Associate PDs were recruited: Riley Bernard and Luis Víquez-Rodríguez (both former student board members) in 2016 and Emma Wilcox (local co-host for NASBR 47 in Knoxville) in 2018.

1.4 Business Meetings

The annual meeting traditionally has been the venue for the membership to conduct the business of the Symposium and now the Society. The Board of Directors started meeting on the Wednesdays before the formal commencement of technical sessions at NASBR 30 (Miami) in 2000. To keep the membership informed of decisions made by the Board, a business meeting was introduced between the morning technical sessions. Initially, the annual business meeting was on Saturday. Subsequently, the Society's growth and complexity required the Board to develop and adopt the current format of two business meetings before lunch on both Friday and Saturday.

At the business meetings, nominations from the floor are accepted to add to the list of candidates compiled by the Nomination Committee for student and regular Board members. Members then vote for regular and student Board members. Also, venue bids for future meetings are presented and voted for, changes to the Constitution and By-laws are debated and voted on, and meeting announcements are made. Since the Board now conducts business year-round, the annual business meetings are a means for the Board to communicate with membership about its decisions regarding the organization, informing the members of previous and future activities, and reporting current financial activity and health. They also serve as venues for members to voice concerns, ask questions, and make suggestions for Board actions.

1.5 NASBR Awards

1.5.1 Student Presentation Awards

From our mission statement, the society "promotes the study and conservation of bats by facilitating communication and collaboration among scientists, educators, and the general public" and students are essential for current productivity and for future efforts of this objective. The society places a high value on student engagement at annual meetings. At the NASBR 13 in Louisville (1982), student honoraria sessions first appeared as the opening of the program, a tradition that has continued to the present. Generous sponsors have donated monetary awards given to students for the best oral and poster presentations, as chosen by an honoraria committee. Over the years the number and types of awards have grown, with ten student awards distributed at the 49th meeting in Kalamazoo. The student awards include the Bernardo Villa Award, the recipient of which is chosen before the meeting, since that award includes meeting expenses and the student's presentation is a component of the plenary session. The other student awards currently are funded by Bat Conservation International, Bat Research News, NASBR Koopman fund, Lubee Bat Conservancy, Titley Electronics, Avinet, Batgoods, Basically Bats, and Indiana State University Center for Bat Research, Outreach, and Conservation.

1.5.2 Gerrit S. Miller Award

This award is presented occasionally at the annual meeting to persons in recognition of outstanding service and contribution to the field of chiropteran biology. The award is named after Gerrit S. Miller, Jr., an outstanding bat biologist of the early twentieth century who was Curator of Mammals at the United States National Museum from 1909 to 1940. Miller's work on the evolutionary relationships of Chiroptera still strongly influences taxonomic thinking today. His most widely read book was entitled "The Families and Genera of Bats", published in 1907, while he was Assistant Curator of Mammals working under C. Hart Merriam.

The first Miller Awards were bestowed in Ottawa at NASBR 8, when Roy Horst and Karl Koopman were presented with plaques recognizing their contributions and service to advancing studies of bats. Roy Horst served as secretary for the Miller Committee until 2014, when Mark Brigham was selected as secretary. The Miller Committee adopted a policy of secrecy, where upon the next recipient's identity remained secret until the annual banquet. All previous winners of the Miller Award are members of the Miller Committee. Although the Miller Award is considered the highest honor within NASBR, it has been until recently the only award not under the purview of the Board. In 2018, an agreement between the Miller awardees and Board made the Miller Award an official committee of the society, chaired by the NASBR Board Chair, who only votes to break a tie. To date there have been 26 Miller awardees, including six female and nine non-United States individuals (Table 1.2).

1.5.3 Lifetime Member Award

Lifetime membership in NASBR is conferred in recognition of a long and distinguished career in service to the Society and bat research or education about bats. Recipients include James Findley (deceased) who was on the program committee of the first meeting, LH of the second meeting, and LH in 1978; Margret Griffiths was LH in 1996 and Associate PD from 1999 to 2005; Tom Griffiths was LH in 1996 and PD from 1996 to 2005; Roy Horst was PD from 1970 to 1995 and 2008 to 2009, received the Miller Award in 1977, Board member in 2000, and LH in 1995 and 2002; Tom Kunz received the Miller Award in 1984, was LH in 1995, and Board member from 2000 to 2001; Merlin Tuttle received the Miller Award in 1986 and was LH in 1992; and John Winklemann was Board member from 2007 to 2009 and Treasurer from 2007 to 2008.

1.5.4 G. Roy Horst Award

Established in 2014, the Distinguished Service Award, or G. Roy Horst Award, is given for significant and consistent contributions to the Society. This NASBR award is named in honor of the sole Program Director and meeting organizer for the first 25 years of the society. The only recipient of this award to date is Pat Morton, founder and coordinator of the Teacher Workshop for over 20 years.

1.5.5 Spallanzani Award

The Spallanzani Award assists distinguished bat researchers from outside North America to attend a NASBR meeting. Lazzaro Spallanzani (1729–1799) was an Italian biologist and physiologist who made important contributions to the experimental study of anatomy, physiology, animal reproduction, and was instrumental in discovering the mechanism of animal echolocation. Spallanzani is mostly known for his experiments on bat navigation in complete darkness, concluding that bats use sound and their ears for navigation. His hypothesis of the echolocation ability of bats

Table 1.2 North American Society for Bat Research (NASBR) Miller awardees

Name	Year presented	Site	Affiliation
Gerald Wilkinson	2019	NASBR 49, Kalamazoo, MI	University of Maryland
Tigga Kingston	2017	NASBR 47, Knoxville, TN	Texas Tech University
Sharon Swartz	2016	NASBR 46, San Antonio, TX	Brown University
Betsy Dumont	2014	NASBR 44, Albany, NY	Amherst University
James Simmons	2013	NASBR 43, San Jose, CR	Brown University
Elizabeth Kalko[a]	2011	NASBR 41, Toronto, ON	University of Ulm
Gareth Jones	2011	NASBR 41, Toronto, ON	University of Bristol
Wieslaw Bogdanowicz	2010	NASBR 40, Denver, CO	Museum & Institut of Zoology PAS, PO
Robert J. Baker	2009	NASBR 39, Portland, OR	Texas Tech University
Nancy Simmons	2008	NASBR 38, Scranton, PA	American Museum of Natural History
R. Mark Brigham	2006	NASBR 36, Wilmington, NC	University of Regina
Rodrigo Medellin	2004	NASBR 34, Salt Lake City, UT	Universidad Nacional Autonoma de México
Robert M. R. Barclay	2002	NASBR 32, Burlington, VT	University of Calgary
Patricia W. Freeman	2001	NASBR 31, Victoria, BC	University of Nebraska
Theodore H. Fleming	1999	NASBR 29, Madison, WI	University of Miami
Gary F. McCracken	1997	NASBR 27, Tucson, AZ	University of Tennessee
Paul A. Racey	1995	NASBR 25, Boston, MA	University of Aberdeen
Don E. Wilson	1992	NASBR 22, Sherbrooke, QC	National Museum of Natural History
Bernardo Villa-Ramirez	1990	NASBR 20, Lincoln, NE	Universidad Nacional Autonoma de México
Merlin D. Tuttle	1986	NASBR 16, Amherst, MA	Bat Conservation International
Harold B. Hitchcock	1986	NASBR 16, Amherst, MA	Middlebury College
Thomas H. Kunz	1984	NASBR 15, Rockford, IL	Boston University

(continued)

Table 1.2 (continued)

Name	Year presented	Site	Affiliation
M. Brock Fenton	1982	NASBR 13, Louisville, KY	Carleton University
William A. Wimsatt	1981	NASBR 12, Ithaca, NY	Cornell University
Donald R. Griffin	1979	NASBR 10, St. Louis, MO	Rockefeller University
Karl F. Koopman	1977	NASBR 8, Ottawa, ON	American Museum of Natural History
G. Roy Horst	1977	NASBR 8, Ottawa, ON	State University of New York, Potsdam

[a] Posthumously

was not fully understood for well over a century until 1941, when Donald R. Griffin first described bat's sensitivity to high-frequency sound.

The Spallanzani Committee can select one or more fellows (Table 1.3) per year, based on available funding, which comes primarily from auction proceeds during the annual meeting. Two types of Spallanzani Fellowships may be awarded: (1) Senior Fellows, for recognition of a career of distinction in research, education or conservation biology of bats that has contributed to the development of these activities in their country; and (2) Fellows, for persons of any age or career stage that show recent meritorious accomplishments that promote bat research, education, and/or conservation programs in their country.

1.5.6 Bernardo Villa Award

The Bernardo Villa award is bestowed upon a Latin American student enrolled at a Mexican university who is deemed to be conducting outstanding research. Bernardo Villa-Ramírez was a Mexican mammologist who studied bats, rodents and marine mammals. He was well known for *Los Murciélagos de México*, a book that became a standard reference for Mexican bat researchers. This award is supported by a fund initiated by former board member Dixie Pierson in 2006 that provides the resources for a student to present their findings at a NASBR meeting, including travel, lodging, banquet, and registration fees. The student's research may be from anywhere in Latin America or the Caribbean, however, priority will be given to those with research emphasis in Mexico. It has been awarded 13 times to 8 female and 5 male recipients (Table 1.4).

Table 1.3 North American Society for Bat Research (NASBR) Spallanzani awardees

Name	Year awarded	Site	Affiliation
Vu Dinh Thong	2019	NASBR 49, Kalamazoo, MI	Vietnam Academy of Science & Technology, Vietnam
Ludmilla Aguiar	2017	NASBR 47, Knoxville, TN	University of Brasilia, Brazil
Pipat Soisook	2016	NASBR 46, San Antonio, TX	Prince of Songkla University, Thailand
Rubén Barquez	2015	NASBR 45, Monterey, CA	University of Tucumán, Argentina
Paul Webala	2015	NASBR 45, Monterey, CA	Massai Mara University, Kenya
Sigit Wiantoro	2014	NASBR 44, Albany, NY	Indonesian Institute of Sciences, Indonesia
G. Marimuthu	2013	NASBR 43, San Jose, CR	Madurai Kamraj University, India
Luis Aguirrre	2012	NASBR 42, San Juan, PR	Universidad Mayor de San Simón, Bolivia
Elena Godlevska	2012	NASBR 42, San Juan, PR	Schmalhausen Institute of Zoology, Ukraine
Diego Tirira	2012	NASBR 42, San Juan, PR	Mamiferos & Conservation Foundation, Ecuador
Emanuel Cristian Mora Macías	2011	NASBR 41, Toronto, ON	Havana University, Cuba
Sara Bumrungsri	2010	NASBR 40, Denver, CO	Prince of Songkla University, Thailand
Pascual J. Soriano	2009	NASBR 39, Portland, OR	Universidad de los Andes, Venezuela
Robert Kityo	2008	NASBR 38, Scranton, PA	Makerere University, Uganda
Lim Boo Liat	2007	NASBR 37, Merida, MX	World Health Organization, Malaysia
Ara Monadjem	2007	NASBR 37, Merida, MX	University of Swaziland, Swaziland
Gilberto Silva Taboada	2007	NASBR 37, Merida, MX	Museo Nacional de Historia Natural, Cuba

1.5.7 Thomas H. Kunz Award

Established in 2018, this award recognizes and celebrates exemplary contributions to the study of bats as well as measurable impacts on bat conservation, student mentoring, public education, and global collaborations by an early to mid-career bat researcher. This award is named in honor of Professor Thomas H. Kunz for his long and distinguished international career in bat biology, ecology, and conservation that inspired many people and strongly promoted positive attitudes towards bats. The

Table 1.4 North American Society for Bat Research (NASBR) Bernardo Villa awardees

Recipient	Year awarded	Site	Affiliation
Yocelyn Gutiérrez Guerrero	2019	NASBR 49, Kalamazoo, MI	Instituto de Ecología, UNAM[a]
Aline Méndez Rodríguez	2018	NASBR 48, Puerto Vallarta, MX	Universidad Autónoma Metropilitana, Campus Iztpalapa
Stephanie Ortega García	2017	NASBR 47, Knoxville, TN	Instituto de Investigaciones en Ecosistemas y Sustentabilidad, UNAM
Beatriz Daniela Carmona Ruiz	2016	NASBR 46, San Antonio, TX	ENCB, Instituto Politécnico Nacional
Crysia Marina Rivero Hernandez	2015	NASBR 45, Monterey, CA	Instituto de Ecología, UNAM
Roberto Salazar Trejo	2014	NASBR 44, Albany, NY	Instituto de Ecología, UNAM
Giovanni Hernández Canchola	2013	NASBR 43, San Jose, CR	Facultad de Ciencias, UNAM
Mariana Zarazúa Carbajal	2012	NASBR 42, San Juan, PR	Instituto de Investigaciones en Ecosistemas & Sustentabilidad, UNAM
Arely Hernandez Dávila	2011	NASBR 41, Toronto, ON	ENCB, Instituto Politécnico Nacional
Jorge Ayala Berdón	2010	NASBR 40, Denver, CO	Instituto de Investigaciones en Ecosistemas & Sustentabilidad, UNAM
Fabricio Villalobos	2009	NASBR 39, Portland, OR	Centro de Investigaciones en Ecosistemas, UNAM
Bernal Rodríguez Herrera	2007	NASBR 37, Merida, MX	Instituto de Ecología, UNAM
Ragde Sánchez	2006	NASBR 36, Wilmington, NC	Instituto de Ecología, UNAM

[a] Universidad Nacional Autónoma de México

first recipient was planned for the 50th anniversary celebrations in 2020 at Tempe, Arizona, but the coronavirus pandemic has delayed this until next year.

1.6 Teacher Workshop

The Teacher Workshop is a yearly event created in 1996 to provide educators in the city where the Society meets with information, training, and activities about bats that are designed to be shared with students of all ages. Local teachers are invited to attend this unique opportunity to learn about bats and how to integrate topics on bat biology, ecology, conservation, and public health into their classroom curricula. The first workshop as an outreach effort for local educators occurred at NASBR 26 in Bloomington and was organized and coordinated by Pat Morton and Jackie Belwood. Pat continued to provide this outreach service for the next 20 years.

Precursors to the Teacher Workshop included a workshop organized by Brock Fenton in Gainesville (NASBR 23) called "Educating the Public about Bats" and a "Conservation Education Workshop" convened by Pat at NASBR 25 in Boston.

1.7 Auction

The annual auction is a fund-raising activity that has seen the sale of a range of items from artwork to books (rare, valuable, or popular) to bat memorabilia to research equipment to trinkets to simply junk (with the hope it becomes a valuable find to someone). The annual auction had its origin with Mark Brigham as a way to raise money for funding travel and conference support for Spallanzani Award recipients. A silent auction component with items on display closes during the banquet. A live auction is usually part of the banquet festivities (initiated at NASBR 35 in Sacramento) or as part of a special reception (as in Scranton, NASBR 38). Due to decreasing funds and lack of donations into the Bernardo Villa Fund, the auction monies are now shared between the Spallanzani and Bernardo Villa Fund.

1.8 Summary

The annual meetings of the North America Society for Bat Research have served as a forum for the presentation and discussion of research about bats. In the 50 years since the first meeting, the growth of NASBR from an informal group of southwestern United States bat biologists to a formal society attracting an international audience of chiropterologists has been substantial. Attendance has grown from 42 individuals at the inaugural meeting to approximately 350–400 now attending regularly. The number of technical presentations has grown from a low of 26, at the inaugural meeting, to consistently numbering approximately 200 in the last decade, excluding years of combined IBRC and NASBR meetings, with the peak number (226) reached in Monterrey (NASBR 45). Two trends were evident to us in reviewing the programs from meetings: a noticeable increase in the number of presentations, particularly after the introduction of posters in 1989 (NASBR 19), and coincidental with the increase in the number of presentations was an increase in the number of presentations by, and attendance of, women at the annual meetings beginning in the third decade of NASBR (Frick et al. 2021).

The open and inclusive nature of our symposia have served as the means for NASBR to conduct its business and prepare for the primary function of the society: to conduct an annual meeting for dissemination of information about bats. NASBR has given a sense of a chiropteran community with an inclusive and international reach. The annual symposium of bat biologists has led to collaborative research among members, fostering development of students and young scientists, championing conservation and educational issues, and building a financially secure society. The camaraderie has been aided by many informal activities, as well as by small formal (technical sessions) and informal discussion groups that occur around the venues of annual meetings. The future looks bright for continued growth of NASBR and we look forward to many more stimulating presentations that will further develop research on bats and our understanding of these unique and fascinating mammals.

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Chapter 2
Contributions of Women and Creating a Culture of Inclusivity at the North American Society for Bat Research

Winifred F. Frick, Amy Russell, and Erin H. Gillam

Abstract The North American Society for Bat Research (NASBR) began in 1970 at a turning point in history for women's rights. Participation by women in NASBR has risen steadily over the society's history, reflecting societal shifts of reducing barriers to advancement and achievement by women in science. Gender parity has been achieved in all forms of presentation type at NASBR (general and student oral presentation and poster sessions). The 50% milestone of women participants in the general oral presentations and as session chairs was only reached in 2015, whereas women have represented the majority of participants in student sessions since the 1990s. The current culture of inclusivity and support for gender and racial diversity in the NASBR society is viewed as generally positive based on a survey of NASBR affiliates. The current Society and annual NASBR meeting have made visible efforts to offer opportunities for raising awareness and discussion around diversity, provide mentoring opportunities, and codified expectations of behavior to create a safe and inclusive conference environment for all participants. Over the past 50 years, NASBR has not only supported and advanced research on bats but has grown as a society to reflect values of inclusion and support for all people working to advance research on bats.

Keywords Conferences · Diversity · Gender nonconforming people · Inclusivity · STEM · Women in science

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2.1 Introduction

As the North American Society for Bat Research (NASBR) reaches the milestone of its 50th meeting, it is important to reflect on how the organization has changed since its inception in 1970, in an effort to identify areas of success toward building a diverse and inclusive society, while targeting areas in need of further growth and improvement. While one can measure the quality and accomplishments of a professional organization based on multiple metrics, a critical feature is how members treat each other, specifically in regard to inclusivity and support of women, racial diversity, and other historically marginalized groups. Creating an environment in which all individuals regardless of gender, sexual orientation, race, ethnicity, or disability feel welcomed and supported in a conference setting and as members of a diverse research community should lead to a better environment for the exchange of ideas and higher participation in the society and science. Here, we examine both historical trends of participation of women in NASBR across its 50-year history and focus on the current attitudes and perspectives of NASBR participants relative to inclusivity and support of gender and racial diversity.

We acknowledge that our context for understanding the cultural environment and change in NASBR over the past 50 years is viewed predominantly through the lens of United States history. NASBR primarily represents researchers from the United States of America (USA), Canada, and México, yet the meeting during its early years was mostly hosted in the USA. In the first two decades of NASBR, only three meetings were held in Canada (1977 in Ottawa, 1987 in Toronto, and 1988 in Calgary), and the first NASBR meeting held in México did not occur until 1994 in Ixtapa, Guerrero. While the society has always welcomed participation from researchers in other regions and has held several joint meetings with the International Bat Research Conference, a more extensive examination of societal changes in the context of world history is beyond our scope.

The first NASBR meeting was held in Arizona in 1970 during the era of the civil rights and women's liberation movements that were fighting for awareness and equality in the United States alongside similar efforts for change and awareness in Canada and México. The gay rights movement was only dawning, as was more general awareness of access and equality for different marginalized groups and people with disabilities. In the United States, 1970 was the 50th anniversary of the passage of the 19th amendment, which guaranteed women's right to vote. In August of 1970, a national Women's Strike for Equality was held that included 50,000 women marching in Washington DC, as well as strikes and protests in major cities across the country. The women's liberation movement succeeded in raising awareness, shifting cultural norms, and providing incentive for key regulatory changes in the United States that removed some institutional barriers for women. Most notable was the passage of Title IX in 1972, which outlawed sex discrimination in any educational program that received federal financial aid. Women's participation in higher education and professional careers has steadily increased since the early

1970s in the United States. Thus, NASBR began at a pivotal moment of change for women in US history.

For our retrospective analysis of participation and representation in NASBR, we focus on women, in part because it is generally possible to infer gender from names listed in conference programs and in part because we have a specific interest in the contributions and participation of women in our academic society. To examine patterns of participation by women in the annual conference, we turned to the record consistently available for all meetings—conference programs. Oral presentations have been the main forum of idea exchange at NASBR and provide the longest time-series to evaluate trends in participation. We also consider trends in authorship across the four main forms of presentations at NASBR, including the general oral presentations and poster sessions, which include members from all professional levels, and the student competition presentation and poster sessions, which focuses on participation at junior levels of professional careers. We examined representation among session chairs, which are invited positions and potentially indicate the extent to which women were viewed as experts in a field. Likewise, we considered the proportion of women asked to participate as mentors in NASBR's Lunch with a Mentor program since 2008. We also assessed participation of women serving on the board of directors of NASBR since 1999 when the board of directors for NASBR was formalized. Lastly, we consider the number of women as recipients of NASBR's significant awards.

Although we were explicitly interested in the contributions of women to NASBR, we also had a broader interest in understanding how NASBR supports a culture of inclusivity of all aspects of diversity. We were not able to examine historical patterns of participation for other aspects of diversity because demographic data have not been collected on participants over most of the history of the society. However, when we examined attitudes of the current society, we broadened our focus to include assessment of inclusivity and supportiveness for not only women, but also for racial and gender diversity. From these data, we expected to gain a clearer picture of where the society currently stands and identify priorities for the future of NASBR.

2.2 Methods

2.2.1 Participation of Women over NASBR's 50-Year History

We evaluated participation by women at NASBR from its commencement year through 2018 by tallying the number of women and men session chairs and authors (first author or presenting author, if indicated separately) of general presentations, general posters, student competition presentations, and student competition posters. We scored all programs except for 1978, 1995, 2007, and 2013 when the NASBR meeting was paired with the International Bat Research Conference (IBRC). In addition, NASBR was not held in 1985 due to member interest in attending that year's IBRC in Aberdeen, Scotland. We also tallied the number of women awardees for five NASBR recognition awards: the Gerrit S. Miller Jr. Award, NASBR Lifetime Member Award, G. Roy Horst Award, Bernardo Villa Award, and the Spallanzani Award.

We inferred gender based on first names of authors listed in conference programs. In cases where initials were used or first names were ambiguous, we performed an internet search and contacted co-authors to confirm gender identity. We identified all first/presenting authors in 34/45 programs for general oral presentations, 21/31 programs of general posters, 27/31 programs for student competition presentations, and 17/20 programs for student competition posters. We ensured there were no more than two first/presenting authors of undetermined gender in each category for each year. Although this data structure inherently reinforces a gender binary framework, we found evidence of only a single individual who might identify elsewhere along the gender spectrum.

2.2.2 Current Attitudes About Inclusivity and Supportiveness of the NASBR Society

To assess the opinions of NASBR members on the society's inclusivity and supportiveness of different groups, we conducted an online survey using Survey Monkey in August 2019. The link to the survey was distributed to the list of all NASBR contacts, which included 925 email addresses. Given the likelihood of some duplicate users with different email addresses, we estimated that the survey link reached approximately 875 individuals. The survey contained a mix of Likert-scale response and open-ended questions. Questions were focused on rating NASBR's inclusivity and supportiveness of women (both cis- and transgender), gender nonconforming people in general, and racial diversity, as well as assessing how this pattern has changed in the last 10 years and what the society could do moving forward to further create a welcoming environment for diverse participants. Information was also gathered about the gender identity and annual household income of the respondents. Results of Likert-scale questions are reported in their raw form, while open-ended responses were scored into one of multiple categories by one of the authors (EHG).

2.3 Results

2.3.1 Participation of Women over NASBR's 50-Year History

The proportion of women participants in NASBR has grown steadily over the past 50 years (Table 2.1; Fig. 2.1). Women authors accounted for less than one quarter of oral presentations for most of the first two decades of NASBR. Participation

Table 2.1 Proportion of women in five categories of participation type at the North American Society for Bat Research (NASBR) from 1970 to 2018

Year	General oral presentations	Student oral presentations	General posters	Student posters	Session chairs	Board of directors
1970	4% (1/26)	–	–	–	0% (0/3)	
1971	8% (3/38)	–	–	–	0% (0/5)	
1972	9% (4/46)	–	–	–	20% (1/5)	
1973	21% (8/39)	–	–	–	14% (1/7)	
1974	14% (5/36)	–	–	–	12% (1/8)	
1975	25% (7/28)	–	–	–	25% (1/4)	
1976	13% (6/46)	–	–	–	–	
1977	11% (4/35)	–	–	–	0% (0/7)	
1978	–	–	–	–	–	
1979	13% (7/53)	–	–	–	12% (1/8)	
1980	19% (6/31)	–	–	–	29% (2/7)	
1981	22% (14/63)	–	–	–	0% (0/7)	
1982	6% (2/31)	27% (3/11)	50% (4/8)	–	12% (1/8)	
1983	15% (3/20)	–	–	–	0% (0/5)	
1984	17% (6/36)	29% (2/7)	–	–	0% (0/8)	
1985	–	–	–	–	–	
1986	26% (9/35)	–	0% (0/2)	–	0% (0/5)	
1987	25% (6/24)	30% (3/10)	–	–	0% (0/5)	
1988	32% (10/31)	33% (4/12)	36% (4/11)	–	17% (1/6)	
1989	28% (11/40)	56% (9/16)	14% (1/7)	–	17% (2/12)	
1990	18% (7/39)	69% (9/13)	55% (6/11)	–	8% (1/12)	
1991	27% (15/55)	37% (7/19)	54% (7/13)	–	19% (3/16)	
1992	19% (8/43)	61% (14/23	10% (1/10)	–	9% (1/11)	
1993	32% (19/59)	50% (9/18)	25% (5/20)	–	23% (3/13)	
1994	24% (17/72)	–	13% (2/15)	–	18% (2/11)	
1995	–	–	–	–	–	
1996	34% (17/50)	42% (5/12)	42% (5/12)	–	12% (1/8)	

(continued)

Table 2.1 (continued)

Year	General oral presentations	Student oral presentations	General posters	Student posters	Session chairs	Board of directors
1997	39% (24/61)	33% (5/15)	46% (11/24)	–	8% (1/13)	
1998	31% (15/48)	57% (13/23)	52% (13/25)	75% (3/4)	0% (0/11)	
1999	29% (15/52)	61% (17/28)	33% (6/18)	33% (5/15)	25% (3/12)	33% (2/6)
2000	22% (11/50)	69% (24/35)	36% (5/14)	37% (7/19)	15% (2/13)	33% (2/6)
2001	37% (26/71)	44% (12/27)	20% (3/15)	74% (14/19)	29% (5/17)	50% (3/6)
2002	42% (28/66)	40% (8/20)	62% (18/29)	62% (8/13)	24% (4/17)	50% (3/6)
2003	36% (19/53)	63% (12/19)	45% (14/31)	31% (4/13)	15% (2/13)	33% (2/6)
2004	43% (35/81)	56% (9/16)	45% (21/47)	38% (3/8)	25% (5/20)	33% (2/6)
2005	48% (41/85)	53% (10/19)	57% (25/44)	45% (5/11)	16% (3/19)	33% (2/6)
2006	39% (29/74)	56% (15/27)	53% (26/49)	64% (9/14)	25% (4/16)	50% (3/6)
2007	–	–	–	–	–	50% (3/6)
2008	43% (49/113)	61% (14/23)	48% (19/40)	57% (8/14)	29% (7/24)	33% (2/6)
2009	48% (44/91)	78% (21/27)	48% (25/52)	57% (4/7)	12% (2/16)	29% (2/7)
2010	42% (30/72)	63% (12/19)	45% (25/56)	56% (5/9)	29% (7/24)	25% (2/8)
2011	39% (42/108)	74% (17/23)	61% (22/36)	58% (11/19)	31% (10/32)	33% (3/9)
2012	47% (38/81)	60% (15/25)	60% (21/35)	71% (10/14)	36% (12/33)	33% (3/9)
2013	–	–	–	–	–	22% (2/9)
2014	48% (44/91)	61% (28/46)	73% (24/33)	79% (27/34)	36% (13/36)	33% (3/9)
2015	53% (57/107)	66% (27/41)	67% (35/52)	85% (22/26)	47% (21/45)	33% (3/9)
2016	53% (43/81)	76% (28/37)	60% (27/45)	70% (16/23)	58% (21/36)	33% (3/9)
2017	60% (50/84)	62% (20/32)	64% (23/36)	63% (19/30)	44% (15/34)	56% (5/9)
2018	59% (49/83)	71% (34/48)	60% (21/35)	64% (27/42)	61% (22/36)	67% (6/9)

Years without data include five occasions when NASBR was paired with the International Bat Research Conference or not held

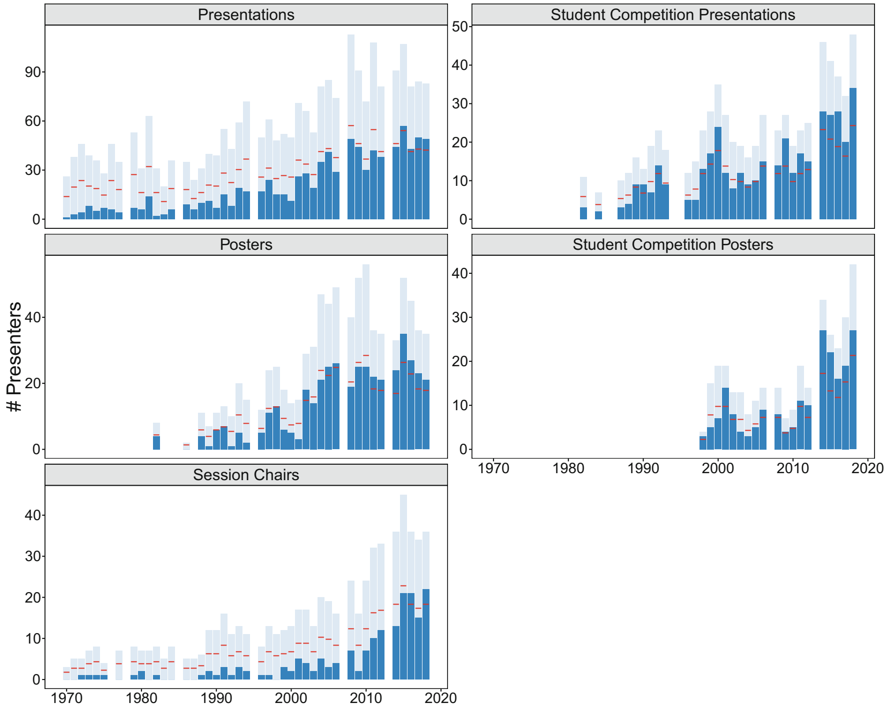

Fig. 2.1 The number of women relative to the total number of first/presenting authors for five categories of participation at the North American Society for Bat Research: general oral presentations, student competition presentations, general poster presentations, student competition poster presentations and session chairs. *Red* lines visually indicate 50% since length of each bar is scaled to total number of presenters. Where *solid blue* bars do not reach the *red* line, participation of women was below 50% and where *solid blue* bars are above the *red* line, participation of women exceeds 50%

increased to 20–30% of talks during the late 1980s and 1990s. Since the early 2000s, women authors have consistently accounted for over a third of general presentations and edged closer to 50%, yet women did not give 50% of general session talks until 2015. Participation in the general poster session was variable in the late 1980s and 1990s when poster sessions became incorporated into the meeting, but has consistently hovered around 50% since the early 2000s. Since 2011, participation by women has exceeded 60% in the general poster session.

Participation by women has been markedly higher in the student competition presentation and poster sessions than in the general sessions. Student competition sessions started in the mid to late 1980s for oral presentations and late 1990s for poster sessions. In 21/30 years of student competition oral presentations, women exceeded 50% of participants and over the past 10 years have consistently accounted for over 60% of student talks, sometimes making up as many as 75% of presentations in this category. Similarly, student poster presentations have been dominated by women since they were started in 1998, with only 5 of 19 years with less than 50% representation and an all-time high of 85% of posters submitted by women in 2015.

In the first 3 decades of NASBR (1970s, 1980s, 1990s), less than a quarter of session chairs were women; in a third of the meetings held in those decades (9 of 26), there were no women session chairs at all. Only since 2015 has there been close to (or greater than) 50% of session chairs held by women.

Women have been active on NASBR's Board of Directors since it was formalized in 1999. The first elected board of NASBR had six board members, two of whom were women (Patricia Freeman and Pat Morton). By 2001, half of the six elected board members were women. Participation dipped and there were minority of women board members from 2010 to 2014, but in the last 5 years early and mid-career women have successfully been elected to the board and the current board now has a majority of women (5/9 elected board members).

2.3.2 Recognition of Women in NASBR Awards

The Gerrit S. Miller Jr. Award is the premier award for contributions to the field of chiropteran biology bestowed by the NASBR society (see Kwiecinski and Horst, this volume). Of the 26 recipients of the Miller award, six have been women and half of these were awarded within the last 5 years. The first woman to receive the award was Dr. Patricia Freeman in 2001 at the 31st NASBR in Victoria, British Columbia. The second woman to receive the Miller award was Dr. Nancy Simmons in 2008 at the 38th NASBR in Scranton, Pennsylvania. Notably, the last three Miller awardees have been women: Dr. Betsy Dumont (2014), Dr. Sharon Swartz (2016), and Dr. Tigga Kingston (2017). Dr. Elizabeth K. V. Kalko was given the Miller award posthumously in 2011.

The NASBR Lifetime member award recognizes long and distinguished careers in research and education about bats. There are only six awardees, including one woman, Dr. Margaret Griffiths, who served the society as the de facto meeting organizer and program director for 10 years. Only one G. Roy Horst Award for outstanding service to the society has been given and the recipient was Patricia Morton for her efforts in hosting the Teacher's Bat Workshop at NASBR for 20 years (1996–2016).

The Bernardo Villa award recognizes an outstanding student researcher from Latin America studying bats at a university in Mexico, providing support for the awardee to present their research at NASBR's annual conference. Since 2006, there have been 13 awards given (not awarded in 2008) with 8 women and 5 men recipients. The Spallanzani Award is extended to distinguished bat researchers from regions outside of North America to attend and give a plenary talk at NASBR. Since its initiation in 2007, there have been a total 15 Spallanzani award winners, only 2 of whom were women (Dr. Ludmilla Aguillar in 2017, and Dr. Elena Godlevska in 2012).

2.3.3 Current Attitudes on Inclusivity and Supportiveness of the NASBR Society

The inclusivity and supportiveness survey that was distributed to the NASBR contact list in August 2019 was completed by 127 participants, which corresponds to a 14.5% response rate, assuming a respondent pool of 875 individuals. Of the participants, 69 (54%) self-identified as cisgender female and 42 (33%) as cisgender male. No participants self-identified as transgender female or transgender male. Thirteen participants selected "prefer not to answer" and three identified as "other—please specify". The gender specified for two of the three individuals choosing this latter category indicated a gender that was available as an option, (for example, one respondent identified their gender as "old white male").

Results of the Likert-scale questions rating the inclusivity of and supportiveness for women (cis- and transgender), gender nonconforming people in general, and racial diversity indicate an overall positive view of the society (Fig. 2.2). Data are presented separately by respondent gender identity—cisgender male, cisgender female, and all respondents pooled (which includes 16 respondents selecting "prefer not to answer" or "other—please specify"). Responses were generally similar across cisgender male and cisgender female respondents for ratings of inclusivity and supportiveness of NASBR for women, gender diversity, and racial diversity. The majority of responses regarding the society's attitude toward women were positive, with 83% of participants ranking NASBR as either "very inclusive and supportive" (58%) or "somewhat inclusive and supportive" (25%). Regarding gender nonconforming people, the most common response was "don't know/unable to assess" (44%). For racial diversity, positive responses were again the most common, with 66% of participants ranking NASBR as either "very inclusive or supportive" (39%) or "somewhat inclusive and supportive" (27%). Negative responses ("somewhat exclusive and unsupportive" or "very exclusive and unsupportive") were generally rare (4% of pooled respondents), but suggest potentially greater concern regarding racial diversity and gender nonconforming people, as these were the only target groups for which any respondents chose 'very exclusive or unsupportive'.

Open-ended questions elaborating on inclusivity and supportiveness for the three target groups were scored into one of six categories: positive, good but more needed, no negative evidence, negative, can't judge, or uncategorized. Not all individuals who answered the Likert-scale questions also answered the open-ended questions. Regarding inclusivity and supportiveness for women, 37 out of 67 (55%) respondents provided positive comments. The percentage of positive comments were lower regarding gender nonconforming people (14 out of 42 respondents, 33%) and racial diversity (13 out of 48 respondents, 27%). For the question addressing changes in NASBR in the last 10 years, responses were scored into seven categories: positive, no change—already positive, no change, mixed, negative, can't assess, or uncategorized. Overall, 41 out of 48 respondents (85%) reported positive change or that the society had always been inclusive and supportive of the three evaluated groups. For the question asking how NASBR might increase inclusivity and

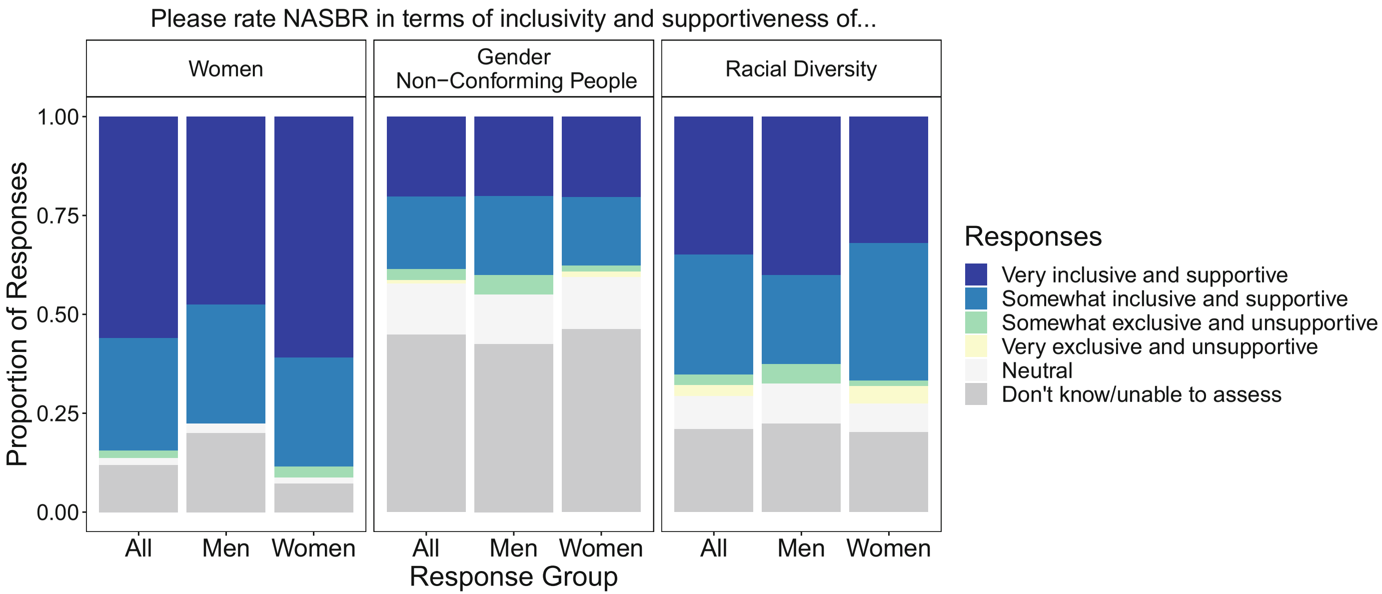

Fig. 2.2 Results of Likert-scale questions to survey participants about inclusivity and supportiveness of women, gender nonconforming people, and racial diversity. The labels at the top of the graph indicate the target group being evaluated (i.e. inclusivity and supportiveness of these groups). The x-axis indicates the gender identity of the respondents, categorized as cisgender male, cisgender female, and all respondents pooled. No respondents identified as transgender, and only 16 of 127 respondents identified as “other” or “prefer not to say”, hence these data are included in the pooled “All” group, but not shown separately due to low sample size

supportiveness for the three evaluated groups, the most common five suggestions were: (1) to increase the number of awards targeting minority groups, (2) to offer workshops by the society related to inclusivity and supportiveness, (3) to implement directed efforts by NASBR to increase diversity at the annual conference, (4) to hold conference events for minority groups, and (5) to continue offering pronoun stickers at future NASBR conferences.

2.4 Discussion

2.4.1 Participation of Women over NASBR's 50-Year History

The rise in participation of women at NASBR over the past 50 years reflects the momentous societal shift toward reducing barriers for women in science that resulted in part from the equal rights movements of the late 1960s and early 1970s, coincident with the inception of NASBR. The trends in participation and representation of women in NASBR tell a generally encouraging story and show that the annual meeting has now achieved parity of participation across all four forms of presentations and among session chairs. Although trends in participation and representation are informative, gender parity in these metrics does not necessarily mean equality of experience for women engaged in bat research, or signal that all barriers to women advancing professionally have been successfully eliminated.

Even now, there is strong evidence of a 'leaky pipeline' problem in STEM fields in academia; the proportion of women scientists falls considerably with advancement in career seniority (Berryman 1983; Hill et al. 2010). In the biological sciences, women earn half of doctorate degrees but hold only a third of tenure-track faculty positions (Hill et al. 2010). Women also tend to account for larger proportions of lower-paying nontenured faculty positions in STEM fields (Hill et al. 2010). The leaky pipeline has many contributing factors, including persistent biases and cultural attitudes regarding women's performance in STEM fields as well as real or perceived barriers to advancing in early career stages that often overlap with child-rearing years (Pell 1996; Darisa et al. 2010).

Historical patterns in NASBR indicate that the Society is consistent with the broader leaky pipeline phenomenon in STEM, as there is greater representation of women at more junior career stages, specifically when comparing participation trends in the student competition sessions to those of the general sessions and session chairs. By 1989, over half of the student competition oral presentations were given by women (56%; 9/16) and both oral and poster student competition sessions have had women as the majority of presenters for the past 15 years (Fig. 2.1; Table 2.1). In contrast, the general oral session did not reach the 50% milestone mark until 2015. Admittedly, parity of participation in the general oral session has hovered just under 50% since the mid-2000s. However, the general session is a mix of career stages, and in the mid-2000s the society changed the rules to limit participation in the student competition session to only once during each degree, which likely increased the proportion of students giving talks in the general sessions and contributed to the achievement of near-parity in the general sessions. Session chairs, which are invited positions on the part of the program directors, did not approach parity until recently (2015), coinciding with efforts within NASBR to raise awareness around issues of women in STEM (see below).

Perhaps one of the most encouraging signs of change is the recent trend toward recognizing the achievements of bat biologists who are women with the Gerrit S. Miller Award. The Miller Award process showcases how inclusion of women often leads to greater recognition of women's contributions. Nominations and decisions to bestow the Miller award have, until recently, been decided entirely by past Miller awardees; beginning in 2019, the award committee is chaired by the chair of the NASBR Board of Directors and nominations are open to the NASBR membership, but voting is still done by past Miller awardees. The first 13 Miller awardees were men, and it was not until 2001 that Dr. Patricia Freeman became the first woman to receive the Miller Award. The applause at the banquet in Victoria, British Columbia, was uproarious with toasts to the shattering of a glass ceiling. It was another 7 years before Dr. Nancy Simmons became the second woman to earn the Miller Award. Since 2008 there has been a notable increase in the number of women recipients, including the past three (2014, 2016, and 2017).

In contrast, the Spallanzani awards remain male dominated, with only 2 recipients out of the past 15 awardees being a woman. The Spallanzani award focuses on bringing a distinguished bat researcher from outside North America to the NASBR meeting. The paucity of women receiving these awards likely reflects global challenges of gender discrimination and barriers to women in science in developing countries around the world. Still, this is an area where the Society can perhaps increase efforts to identify women nominees.

The Bernardo Villa award has seen a majority of women recipients since it became regularly judged and awarded in 2006. Considering that this award targets people (specifically, Mexican students) earlier in their careers, the high proportion of Villa award winners who are women compared to Miller and Spallanzani award winners may further reflect the impact of the leaky STEM pipeline. We are encouraged that the majority of recipients of the Bernando Villa award have been women and that this award has served to support and acknowledge young women scientists in Mexico. This is especially poignant given that the late Dr. Elizabeth Pierson, the fourth woman elected to the NASBR board, worked to establish the Bernardo Villa award during her board term.

2.4.2 Perspectives on the Early Years of NASBR

The early decades of NASBR were male dominated, and women contributing during that period were not only advancing bat research but were breaking glass ceilings for today's aspiring and successful women scientists. Prior to the formation of NASBR, women studying bats would likely have participated in the American Society of

Mammalogists (ASM). A recent review examining the contributions of women to ASM, which turned 100 years old in 2019, showed that participation of women at ASM was scarce prior to 1970, with overall participation in the annual ASM meeting around 5% and authored presentations less than 10% until the late 1960s (Dizney et al. 2019). The context for women participating in academia and academic conferences during the early years of NASBR in the 1970s is perhaps difficult for many of us to imagine today. For firsthand perspective on this period, we interviewed by email two women who were present during those early years to ask about their experiences and to honor their roles as pioneering bat biologists.

Dr. Donna Howell was the only woman who presented her research at the first NASBR in 1970. She was a doctoral student at the University of Arizona in Tucson, where the meeting was hosted that year. Fittingly, her talk focused on the mutualistic adaptations of bat pollinators and their plants in the iconic Sonoran Desert system. Howell had an active but short scientific career, publishing 24 papers from 1970 until the mid-1980s, including some of the seminal papers on bat-plant mutualisms and behavioral ecology of nectar-feeding bats (Howell 1979; Howell and Roth 1981). In addition to being the only woman to present at NASBR in 1970, she was also the first and only woman to chair a session at the 1972 NASBR in San Diego, California. Dr. Howell held an endowed chair at Southern Methodist University before she left academia and worked as a federal and state biologist and contract biologist before retiring from biology altogether. When asked about her experience and memories of NASBR, she wrote: "What I remember is we were all really into our work and had fun sharing and were always mutually amazed at the marvelous stuff our colleagues were discovering". She reflected that she did not realize she was the lone woman at the first NASBR and saw everyone as pioneering bat biologists regardless of gender.

Dr. Patricia Brown has been an attendee at NASBR since 1971 when she first attended as a doctoral student at University of California, Los Angeles, working on ontogeny of vocalizations and echolocation in pallid bats (Brown 1976; Brown et al. 1978; Brown and Grinnell 1980). Dr. Brown has had a long career dedicated to bat biology and conservation and is one of the longest attending members of NASBR. Her career path is one that dispels the mythology of linear career trajectories and reflects a dedication to bats and field biology that transitioned from academic science to consulting biologist. One of her most important contributions to bat biology was raising awareness about the importance of abandoned mines as bat habitat, writing letters and giving presentations to federal agencies in the 1980s. These efforts ultimately helped lead to the creation and funding of Bat Conservation International's Bats and Mines program, which remains active today.

When asked about the early years of her career, Dr. Brown described sexual harassment as commonplace when she was a student in zoology in the 1960s, remembering, "I had to walk a tightrope between alienating the male faculty and falling prey to them." When she began attending NASBR in 1971, there were no women with faculty appointments who worked on bats in the USA and no female mentors at NASBR. While sexual and gender discrimination was rampant within the academic halls, Dr. Brown remembered NASBR as being friendly and encouraging of her research and she felt welcomed. She has personally witnessed changes in

NASBR over the history of the Society. She notes that diversity in interests of attendees began to occur in the 1980s and 1990s as more agency biologists, educators, and consultants began to participate to learn more about bats. Women were better represented in these constituencies during those years and continue to be involved in NASBR. Dr. Brown reflected, “Since I had chosen to enter a male-dominated scientific field over 50 years ago, I accepted gender inequality. I had no women mentors or role models, but I did know some excellent and nurturing men who treated me as an intellectual equal. I am very happy that women are now free to pursue careers other than those designated for women 50 years ago, and that there are women in NASBR who can mentor and support them.”

2.4.3 Current Efforts by NASBR to Support an Inclusive and Diverse Society

Overall, our survey of current NASBR members indicates that the Society is doing well toward creating an inclusive and supportive environment for gender and racial diversity. Further, respondents reported generally positive change in the last 10 years of the Society’s history. For example, one respondent stated “I think NASBR has always been inclusive and supportive, but is doing a better job now of being proactive in these areas. I think that advertising our inclusivity is an important way to signal that we really do care”. Some respondents had specific suggestions of improvements that the NASBR Board of Directors might consider for future initiatives. For example, multiple respondents pointed out that NASBR would benefit from a Diversity committee focused on increasing attendance at the conference by under-represented students and professionals. Some respondents suggested providing child-care at the meeting to support participants, and because this sends a message to students “…that science and family are not mutually exclusive enterprises”.

2.4.3.1 Women and Diversity in Science Breakfast

At the 2013 IBRC/NASBR meeting in San Jose, Costa Rica, a small group of women (including the authors) brainstormed for an idea to provide an opportunity for members of NASBR to engage personally and directly to address challenges for women in STEM. The resulting idea was to provide a forum for awareness and support for women, with a focus on mentoring junior women working to advance their academic careers. We were early to mid-career women supporting each other, and we wanted to expand opportunities for others in the Society. When Amy Russell, who was on the NASBR Board of Directors at the time, proposed the idea for a Women of NASBR event at the annual meeting, it was met with skepticism and uncertainty. Nevertheless, we persisted and, without official recognition in the

Fig. 2.3 Attendees of the diversity in science breakfast at the 48th North American symposium on bat research held in Puerto Vallarta, Mexico

NASBR program, we got the word out to show up Friday morning, commandeered a set of tables in the breakfast room, and held the first "Women in Science Breakfast" event at the 44th NASBR in Albany, New York. Turnout that first year was robust with close to 50 people, including a few men. Since then, the Breakfast has become an official NASBR event, and attendance has grown each year (Fig. 2.3). In 2016 we changed the name to the Diversity in Science Breakfast to broaden the constituency and scope of the event to include discussion on all aspects of diversity beyond gender, including racial diversity and other groups.

The Diversity in Science Breakfast serves as an opportunity for NASBR participants across the spectrum of career stages to discuss topics related to promoting gender and racial diversity in science. The format is small group discussions at breakfast tables. The organizers place suggested topics for discussion at each table with instructions to focus on identifying ways to resolve challenges. The topics vary from year-to-year, but they are related to common themes including imposter syndrome, implicit bias, harassment, international education and collaboration, increasing diversity in STEM, LGBTQ+ issues, and increasing participation of diverse groups in academia. By focusing on small group discussions, participants have a chance to interact directly with other interested people, ranging from first-year students to senior academics. This has proven to be one of the most meaningful outcomes of the event. Students listening to prominent people in our field talking about their own struggles with, for example, imposter syndrome raises visibility and creates a sense of community. The event has also educated our members and raised awareness about these topics. For example, a male professor noted in 2018 that he had never heard of the term imposter syndrome before attending the breakfast despite suffering from it.

The original Women in Science breakfast event in 2014 coincided with the election of three women to the NASBR Board of Directors. The following year at the 45th NASBR in Monterey, California, the proportion of women serving as session chairs rose considerably and approached parity for the first time in the history of the society. Likewise, it was in 2015 that the milestone of 50% of general presentations by women was achieved and the Women in Science Breakfast event was advertised in the official NASBR program.

2.4.3.2 Code of Conduct and Establishment of Ombudspersons

In 2014, several incidents were reported to the NASBR Board of Directors concerning inappropriately sexist or lewd comments and actions during social events at the meeting. In response to this, the NASBR Board of Directors drafted a Code of Conduct for the Society and established ombudspersons for reporting incidents. The Code of Conduct was formally accepted in 2015 and then amended in 2017 when ombudspersons were established to provide guidance and a means to report incidents in safe and anonymous ways. The Code is accessible on the NASBR website (https://www.nasbr.org/conduct). Codifying expectations for behavior is an important declaration of the values of organizations and a key step toward creating an inclusive culture.

2.4.3.3 Lunch with a Mentor

Beginning in 2008, the student representatives on the Board of Directors began coordinating a Lunch with a Mentor program, providing student attendees with the opportunity to meet with a professional over lunch on 1 day of the conference. While not specifically targeting inclusivity, research shows that mentorship is highly beneficial for women and under-represented groups to increase contributions and remain engaged in academic research (Jacobi 1991; Fadigan and Hammrich 2004). The Lunch with a Mentor program provides students with direct access to early, mid, and late career NASBR participants. Conversations often veer from specifics about bat-research to more general topics regarding careers and professional advancement. Over time, the program has grown to include professional consultants, state and federal wildlife managers, and individuals working for non-profit conservation groups, as well as mentors from within academia. Further, the coordinators of the program have made a point to include mentors varying in gender, age, race, ethnicity, and sexual orientation. Records from 2008 to 2019 on participating mentors show consistency in gender parity, with only 2 years when less than 40% of mentors were women.

2.4.3.4 Pronoun Stickers

Following the lead of other scientific societies such as the Ecological Society of America, NASBR made pronoun stickers available at registration beginning at the 2018 meeting in Puerto Vallarta, Jalisco. Available at registration to affix to nametags, the stickers explicitly state a person's pronouns (e.g. "she/her"). The use of pronoun stickers, regardless of gender identity, recognizes that the pronouns used by a person may not be obvious from physical appearance. When used by gender nonconforming people, the stickers convey how a person wishes to be addressed and facilitate comfortable communication; when used by cisgender people, the stickers normalize the introduction of one's pronouns. Availability and adopted use of pronoun stickers are part of NASBR's recent efforts to signal a welcoming and inclusive society, particularly communicating that gender nonconforming people are valuable members of the society.

2.5 Conclusion

Over the past 50 years, NASBR has not only supported and advanced research on bats but has evolved to reflect values of inclusion and support for a diverse community of people who undertake research on bats. In recent years, the society has taken more active and visible steps toward creating a culture of inclusivity and promoting a safe and supportive environment for the exchange of ideas. Much of this book explores how the past 50 years of scientific discovery of bat biology lays the foundation for the next generation of research questions. Similar to how good science leads the way for new discoveries, the past efforts by NASBR to improve inclusion should lead us to continue to work to improve and support a diverse membership. Like science, the work of inclusion is never finished and only sustained attention will continue to build and support a diverse and dynamic society that can maximize the potential for advancing our science about the biology of bats.

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Part II
Echolocation

Erin H. Gillam

Over the last 50 years, we have seen huge leaps in our understanding of echolocation, the sensory system that most bats use to detect the world around them. Our understanding of the neural underpinnings of echolocation call production have advanced substantially, as has our knowledge of how bats adapt their signals in real time to fit their current behavioral and ecological surroundings. In addition, the hardware and software we use to study echolocation has improved by leaps and bounds. Given this progress, it is not surprising that studies of echolocation have had a prominent presence at NASBR conferences, often warranting a dedicated "Echolocation" session. In this section, we explore some of these advances in our understanding of bat echolocation, as well as take a look at how the technology associated with studying these signals has changed over the years.

In Chapter 3, Zamora-Gutierrez et al. examine how the methods used to study echolocation by bats has changed over the last 50 years. From the simple narrowband heterodyne detector favored in the 1970s to the advent of broadband frequency division and time expansion methods through modern full-spectrum units, Zamora-Gutierrez et al. take us through how the technology has changed over the years and what this has meant for the types of research questions that bat biologists have been able to ask. In addition, the authors discuss how analysis of acoustic data has shifted over time, particularly focusing on the increasing sophistication of the methods used to classify unknown echolocation calls to the species level.

In Chapter 4, Smotherman et al. investigate a question that has interested bat biologists for decades—how do bats effectively orient using echolocation in environments that contain noise? The authors discuss powerful laboratory methods that

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allow researchers to understand the neural processing of echoes, as well as both laboratory and field studies that assess how bats acoustically cope with noise. In addition, the authors discuss both lab and field studies examining how the echolocation calls of other bats can be a potential source of acoustic interference.

Chapter 3
The Evolution of Acoustic Methods for the Study of Bats

Veronica Zamora-Gutierrez, M. Cristina MacSwiney G., Santiago Martínez Balvanera, and Everardo Robredo Esquivelzeta

Abstract The study of bat acoustic signals requires specialized equipment with microphones capable of recording high frequencies. There has been growing interest in bat acoustics and a rapid evolution in ultrasonic recording equipment, from the pioneering work using detectors weighing several kilograms, to the current pocket-sized and open source recorders. The increasing accessibility of bat detectors has extended the field of bat acoustics from simple activity detection to acoustic species identification and experimental research. Traditional call analysis was based on multivariate statistical techniques such as discriminant function analysis. However, technological improvements have led to expanding knowledge regarding the complexity and versatility of bat echolocation, and have kindled the evolution of signal processing methods with new approaches (i.e. deep learning) and more powerful computational techniques. Free access to reference libraries that permit adequate and extensive algorithm comparisons have emerged as a cornerstone for the refinement of automated acoustic analysis. Acoustic surveys have provided important insights into the effects of anthropogenic activities and urbanization on bat activity and diversity. Understanding how human activities affect biodiversity is a crucial prerequisite for the development and application of effective species conservation programs.

Keywords Acoustic libraries · Deep learning · Echolocation · Ultrasonic detectors

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3.1 Introduction

Bat surveying and monitoring are becoming crucial to the determination of changes in ecosystems caused by important current threats, such as climate change, land-use change, diseases and deforestation, among others (Voigt and Kingston 2016). Although different techniques, ranging from visual counts to genetic analysis, exist for the study of changes in bat communities, bats have traditionally been studied by implementing capture methods such as mist nets, harp traps and/or hand nets. These methods are popular since they require relatively inexpensive equipment and avoid any potential uncertainty in the posterior species identification. However, capture methods are invasive and stressful for bats, as well as being labor intensive, with trained professionals being required to carry them out. Moreover, they can be applied only in certain habitats (e.g. small water bodies, flyways) and are intrinsically biased towards more easily captured bat groups or guilds (e.g. frugivores, nectarivores), thus creating large knowledge gaps regarding the distribution, ecology and conservation of species that are less easily captured (e.g. molossids) (MacSwiney et al. 2008).

In recent years, acoustic methods—the use of ultrasound detectors to record bat echolocation calls—have gained popularity in bat studies (Adams et al. 2012; Jones et al. 2013; Walters et al. 2013). The advantages of acoustic over capture methods include the ability to set up automatic detectors to record bats without the need to have personnel on site manipulating the equipment and the possibility of documenting bat activity without any direct observation or manipulation. Automatic and remote recording enables the deployment of several units simultaneously and allows the monitoring of bat activity over long periods of time across extensive areas (Hill et al. 2019). The greater survey efficiency and lower cost of acoustic monitoring methods has opened up the opportunity to study other bat groups (e.g. higher-flying aerial insectivores), and to explore a broader and more profound questions regarding bat ecology (e.g. sensory ecology, anthropogenic effects on bat communities, foraging behavior). However, the echolocation calls of some bats are difficult to record because of low intensity or loudness, such as phyllostomids, and other groups do not echolocate, such as pteropodids. So broader studies of community ecology and species diversity would benefit from the complementary methods of acoustic monitoring and live capturing.

The development of bat acoustic studies intertwines biological knowledge with advances in hardware technologies, computational algorithms, statistical applications and data access (Fig. 3.1). The following sections describe this process from the perspective of each of the main axes of change in the recent history of bat acoustics.

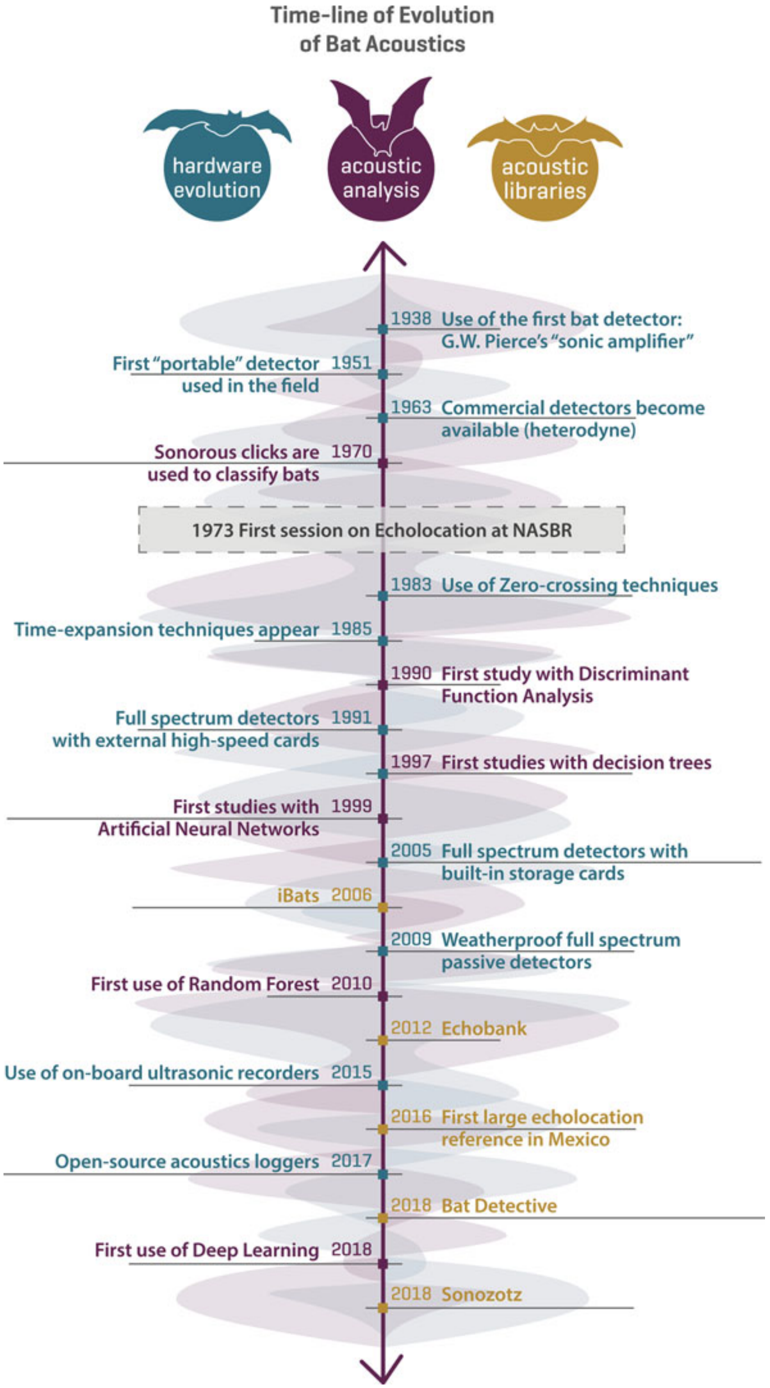

Fig. 3.1 Timeline of the evolution of bat acoustics in terms of hardware, acoustic analysis and the creation of acoustic libraries

3.2 Hardware Evolution

Ultrasonic detectors, or more commonly named “bat detectors”, have advanced considerably since their invention in 1938, when Donald Griffin captured ultrasounds through G. W. Pierce’s “sonic amplifier”, a heterodyne detector with an audio output constructed by modifying an AM radio receiver (Pierce and Griffin 1938, Fig. 3.2a). Since the use of the first bat detector, the need to understand the neurological and ecological aspects related to ultrasound emission by bats has motivated researchers to improve acoustic technology, particularly in terms of microphone quality, recording techniques, and simplicity of data storage (Parsons and Szewczak 2009). Upgrades in microphone technology and the use of oscilloscopes permitted the first representations of echolocation pulses, and the opportunity to obtain measurements from them. These advances opened up a new world of research and were important in the discovery of the mechanisms by which these pulses, and their returning echoes, aided navigation and prey capture during flight. In the early 1950s, Griffin and other researchers assembled a more “portable” ultrasonic detector (in fact composed of several heavy components that had to be carried in vehicles or boats) which permitted the quantification of the variety of in-field echolocation calls of species from different feeding guilds and how these correlate with their ecological niches and behavior (Grinell et al. 2016).

In the 1960s, bat detectors became more accessible to researchers with the appearance of the first commercially available examples (e.g. The Holgate Ultrasonic Receiver, which used a heterodyne system to transform ultrasonic sound into audible sounds, Fig. 3.2b). Heterodyne systems work by multiplying the input signal with an internal fixed-frequency oscillating signal and filtering the result, producing a shift of the input signal into the audible range. Although this system is very sensitive, it can only deal with a narrow bandwidth of the acoustic signals, discarding all other simultaneous bat calls at different frequency bands. The availability of bat detectors propelled a generation of neurobiological studies related to echolocation, as well as surveys of bat activity in different habitats and the understanding of the basic aspects of sound production and reception in bats (e.g. Doppler-shifted compensation). These studies were presented in the early conferences of the North American Symposium on Bat Research (NASBR) during the beginning of the 1970s.

Despite the fact that heterodyne systems were becoming accessible and popular, they had the disadvantage of only being able to monitor a narrow range of frequencies at a time. Likewise, digital full-spectrum recording of bat sounds was restricted by the sampling rate of standard computer audio cards which set the upper frequency limit well below the full spectral range of most species’ echolocation calls. However, at the beginning of the 1980s, advances in technology allowed the development of the first broadband sound transformation technique: frequency division. Ultrasonic detectors using this feature provided better resolution and could retain more information from bat echolocation pulses, enabling the identification and monitoring of multiple bat species targeting different frequency ranges at the same time. Frequency

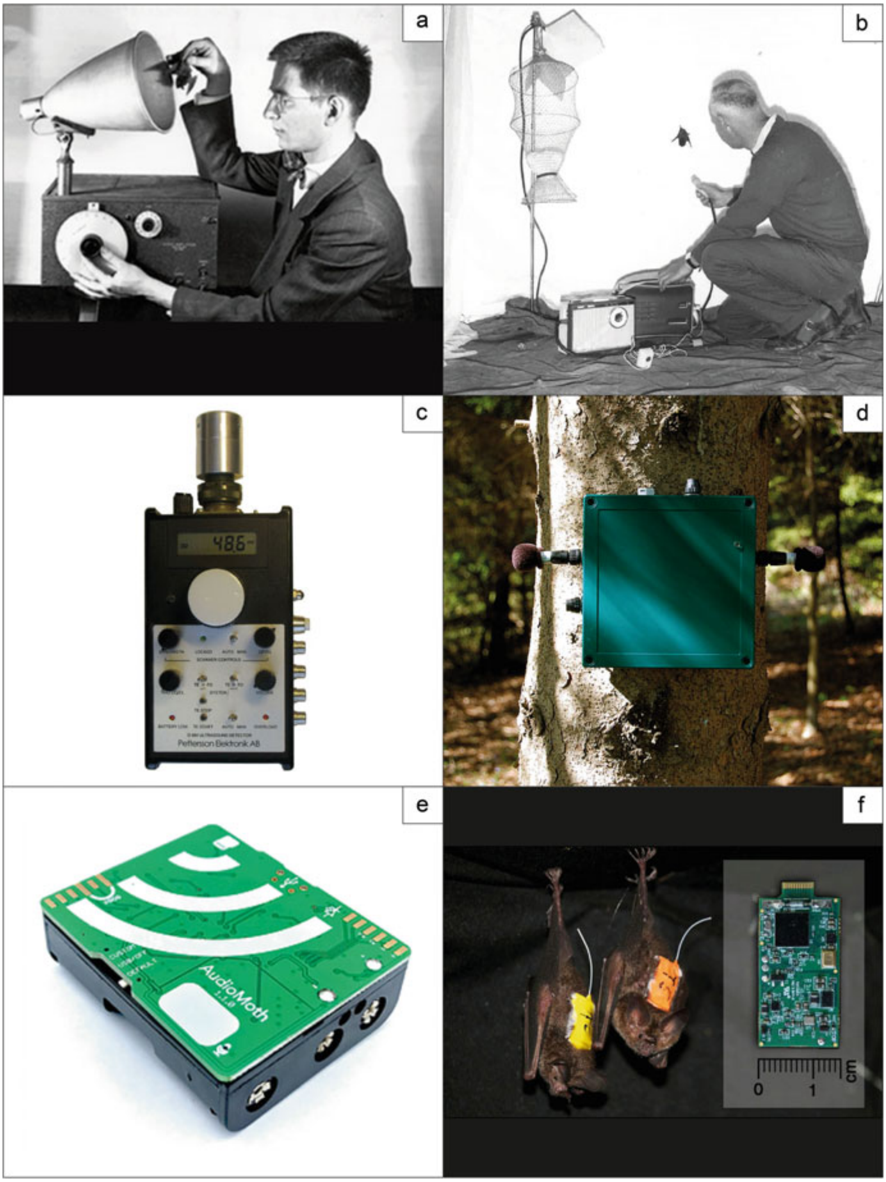

Fig. 3.2 Examples of ultrasonic detectors. (**a**) Pierce's sonic detector. (**b**) Holgate ultrasonic receiver. (**c**) Pettersson D980, bat detector introduced in 1991 that included heterodyne, frequency division and time expansion (×10) systems, as well as high frequency with the use of external high-speed storage cards. (**d**) Song meter SM2BAT, long-term passive bat recorder with waterproof case. (**e**) Audiomoth, open-source acoustic logger. (**f**) On-board microphone "Pipistrell" attached to the fringe-lipped bat *Trachops cirrhosus*

division technique converts the input signal into a square wave, disregarding many aspects of its original shape, and is then fed into a digital frequency divider. The frequency divider counts the number of times the signal crosses the zero reference value and generates one output cycle for every ten zero-crossings (Pettersson 2002). The use of this technique has been very popular to assess habitat use and has been referenced in NASBR meetings from mid-90s until today. Unfortunately, this technique is only able to represent the harmonic with the strongest energy, eliminating any extra acoustic information and other signals produced at the same time (e.g. from other bats), thus limiting the correct identification of certain species (Parsons and Szewczak 2009).

A few years later, the broadband transformation technique known as "time expansion" became available for bat research (Ahlen and Pettersson 1985). This technique allowed ultrasound to be recorded, digitally stored and played back at a lower speed, preserving all the characteristics of the original signal and making them ideal for sound analysis. However, time expansion also showed some difficulties: (1) while expanding the signal (at rates of 10× or 20×), no other signal could be captured, making this procedure impractical for real time and continuous monitoring of bat activity; and (2) these types of detectors were, in general, more expensive than those with heterodyning or zero crossing. Nevertheless, since time expansion was able to retain all of the information from the original call (including all harmonics), it became widely used for acoustic identification of species and in playback experiments (e.g. MacSwiney et al. 2008).

In the early 1990s, real time or high-speed recording became available. Real time recordings were able to register full spectrum signals and, with the aid of computers, high-speed reel-to-reel recorders or external data cards, could be stored and later analyzed without the need of transformation. The possibility of using this recording technique motivated several studies of bat ecology; however, a major limitation was that the equipment was expensive, fragile, bulky and heavy. This all changed during the mid-2000s, when technology permitted the storage of real time signals on built-in cards, considerably reducing their cost and improving portability (Fig. 3.2c). Recording signals in real time with full-spectrum data, a pipe dream since the beginning of acoustic studies, was finally achieved.

Use of real time detectors spread by the end of the 2000s because real time detection components were being incorporated into waterproof cases in a cost effective manner (Fig. 3.2d). These devices allowed recording in the so-called "passive mode", which meant that researchers could leave recorders completely unattended in the field for several days or weeks to gather acoustic information. Another advantage was that multiple recorders could be positioned in different locations in the field at the same time. Massive deployment of passive acoustic sensors helped to answer ecological questions about echolocation behavior, patterns of distribution and habitat use, among others. Soon, several brands of passive recorders with different microphone sensitivities and recording features became available (see Adams et al. (2012) for a comparison of passive detectors). Since then, full-spectrum handheld detector technology has evolved, gaining field portability (lowering weight and increasing durability) and incorporating built-in screens for sonogram display. Some of these devices even have an onboard identification tool, which predicts the identity of the recorded bat in real time.

In recent years, the miniaturization of digital components has permitted the development of low-cost full-spectrum acoustic loggers with a considerable reduction in size (e.g. Audiomoth-Open Acoustic Devices, Fig. 3.2e). These loggers can also be deployed in several locations in the field and are easily customized through applications available on the developer's webpage or directly on mobile telephones. Settings such as recording schedule, gain and sample rates are easily set, and many programs can calculate the device's battery lifespan under a specific configuration (Hill et al. 2019). These loggers have been used to monitor insects, to detect human disturbance (i.e. poaching through gunshot noise) and to survey bat calls in Cuba and Madeira, Portugal. The low cost, practicality and flexibility of open-source acoustic technology, boosted by social network forums with technical support and recommendations, will undoubtedly increase its popularity in the coming years.

Another significant advance in technology has been the miniaturization of on-board ultrasonic recorders which can be directly attached to the body of a bat. One example of these devices is the on-board microphone "Pipistrell", which weighs only about 2 g with batteries included (Yovel pers. comm., Fig 3.2f). Miniature biologgers, which collect GPS location and ultrasonic audio, are already providing accurate and novel information on bat ecology and behavior, such as: (1) location of foraging sites; (2) understanding how bats adjust their echolocation calls to different environmental conditions; (3) social interactions during flight; and (4) the use of bats as mobile sensors in areas inaccessible to researchers, such as high altitudes (Greif and Yovel 2019). In the future, this technology will provide invaluable insights into the sociobiology and ecology of bats.

3.3 Acoustic Analysis and Automatization

The first attempts to extract ecological information from acoustic data in the early 1970s occurred in the context of narrowband detector technology, which presented bat echolocation events as ephemeral sonorous clicks that could not be easily stored (Fenton 1970). The binary on-off treatment of call events was eventually superseded in the 1980s by richer representations from the newly developed broadband detectors. With this equipment, acoustic data could be stored on magnetic tapes and visualized in the time-frequency spectrum by means of an in-field oscilloscope (Simmons et al. 1979). Such advances revealed the complexity of bat echolocation and opened the field to quantitative studies of acoustic characteristics that highlighted the strain between trustworthy detection and multiple sources of acoustic variation (Fenton and Bell 1981).

Early studies of call structure addressed some of the main problems that shaped the future development of bat acoustic analysis, namely the need to understand variation in bat calls in order to establish a set of criteria for a replicable acoustic identification process (Simmons et al. 1979). These studies aimed to find descriptive features of bat calls that could be used to determine the species of the emitter, serving as a prelude to standardized manual classification. Measures such as resting frequency, call duration and peak frequency, among others, were investigated in the search for qualitative features that could separate calls of different species (Simmons et al. 1975; Fenton and Bell 1981; Vaughan et al. 1997; Armitage and Ober 2010). This approach was enriched in the following years with new descriptions of species in terms of acoustic features and further refinement of acoustic descriptors.

Qualitative species identification of unknown bat echolocation recordings relies on homogenous criteria across different observers to be replicable. This condition, along with the hefty labor toll, raised criticism over the feasibility of qualitative methods, which were considered highly subjective (Skowronski and Fenton 2009; Armitage and Ober 2010). The automation of key steps in acoustic analysis, such as feature extraction (e.g. SONOBAT software) and classification, were proposed as tools with which to mitigate observer bias and alleviate workload (Armitage and Ober 2010). Discriminant function analysis was one of the most common methods in the early stages of automated classification of bat calls (Vaughan et al. 1997) but other novel methods, such as decision trees and artificial neural networks (introduced at NASBR 1999), were also tested and compared (Walters et al. 2012). Acknowledgement of similarities between bat vocalization analysis and automatic speech recognition (where targeted acoustic events are phonemes or other phonetic units), a field at the forefront of technical development for automated acoustic processing, showed some convergence to modern views of the broader problem of sound classification (Skowronski and Harris 2006). This motivated the implementation of newer techniques in the study of bat echolocation, such as Hidden Markov Models, Gaussian Mixture Models (Skowronski and Harris 2006) and Random Forests (Zamora-Gutierrez et al. 2016).

In the beginning of the 2000s, the progressive enlargement of acoustic libraries, together with the application of more robust multivariate methods such as those mentioned previously, brought into question the overall need for expert knowledge in the process of classifying bat echolocation calls (Skowronski and Harris 2006). One study from this period found that, on average, an artificial neural network model outperformed human subjects in bat acoustic classification tasks, and even demonstrated little advantage of expertise when comparing between human outcomes (Jennings et al. 2008). Evidence of this kind strengthened the critique of the subjectivity in "expert-driven" approaches and pushed the field into a "data-driven" paradigm. Within this perspective, the observer influence is minimized in favor of the information that data itself can provide, stressing attention to data representativity and sample design for model training and testing (Biscardi et al. 2004; Skowronski and Harris 2006). The adoption of "data-driven" methodologies inherited the challenges and possibilities of generating knowledge in the era of "big data", where information availability is less of an issue and automated data analysis is nurtured by more elaborate machine learning applications and hardware technologies.

Advances in computational parallelism in the last decade ushered in a score of increasingly complex artificial neural network architectures, branded under the term "deep learning". These new models largely surpass any other previous attempts at difficult automated classification tasks, as demonstrated by the overwhelming advantage of the AlexNet model in the ImageNet Large-Scale Visual Recognition Challenge, which consisted of classifying images with highly diverse contents into 1000 target classes (Krizhevsky et al. 2012). The use of deep learning technologies for bat acoustic analysis provides the possibility of capturing subtle characteristics of call structure, circumventing the need for manually designed parameters that could be biased towards ease of interpretation and calculation, but might otherwise be unfit for classification purposes. Such a process consists of feeding large quantities of high-fidelity representations of the acoustic data into an algorithm designed to learn meaningful features for classification. Many of the traditional methods employed for automatic taxonomic classification of bat calls present important deficiencies for some groups (Walters et al. 2012; Zamora-Gutierrez et al. 2016) and deep learning techniques are a new source of alternative approaches. A notable use of deep learning was published only recently in 2018 with BatDetective (Mac Aodha et al. 2018), which harnessed the large and diverse dataset amassed by the "iBats" program to fit the first deep convolutional network for bat call detection, producing encouraging results. Furthermore, the first presentation of any research using "deep learning" techniques at a NASBR meeting was given this same year. Still, these tools have yet to be fully explored.

Comparability of the diverse methodologies in bat acoustic analysis (Fig. 3.3) has remained a key issue ever since call parameters were manually measured from oscilloscope screens (Fenton and Bell 1981). Several studies have noted little concordance between different approaches of automatic bat identification (Russo and Voigt 2016), with a species-level agreement of the commercially available classifier software ranging between 40 and 50% (Lemen et al. 2015). Intrinsic and extrinsic variation in bat sounds, such as geographic, intraspecific and climatic variation, and even differences produced by changes in recording technology, imply that different compilations of field recordings can generate unwanted specificity in trained models, thus impairing their performance when attempting to use them in other contexts (Biscardi et al. 2004). These concerns necessitate the creation and adoption of an evaluation process that can meet the goals of objectivity, transparency and replicability. Diversification and enlargement of open access datasets with compliance to agreed standards and with comprehensive methodological metadata will be an essential step forward. Clear and predefined metrics for model performance comparison are also in dire need. However, global solutions might be unattainable, as suggested by the "No Free Lunch" theorems (Wolpert 2001), and thus the generation of multiple regional models for species classification is ostensibly a better strategy.

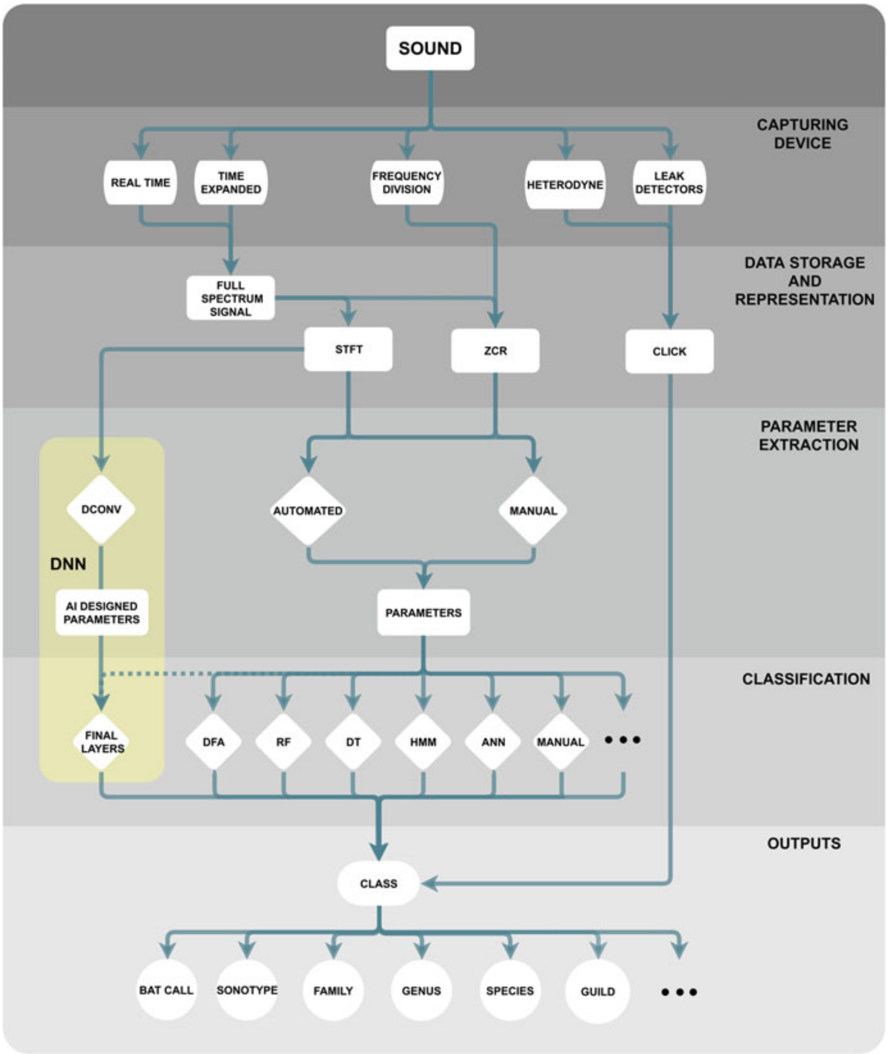

Fig. 3.3 Main processing routes used during the evolution of bat acoustic analysis. Shaded bands represent major phases, from the capture of raw sound events to meaningful classifications. Data flows downwards and top-to-bottom paths represent possible analysis pipelines. The *yellow* box highlights the fact that Deep Neural Network (DNN) methodology merges parameter extraction and classification phases. The dashed line indicates that Artificial Intelligence (AI) designed parameters can be used as inputs of other classification methods and classical parameters can be combined with AI parameters to produce classifications in a DNN. *DCONV* deep convolution, *ZCR* zero crossing rate, *DFA* discriminant function analysis, *RF* random forest, *DT* decision tree, *HMM* hidden Markov model, *ANN* artificial neural network

3.4 Data Compilation and Access

Technological advances led to the widespread use of detectors in bat studies, making way for detailed call descriptions that opened the possibility of species acoustic identification. Although call descriptions began with the creation of the first detectors, efforts towards the compilation of large scale and standardized datasets have been limited (Walters et al. 2013). Most bat reference calls have been collected for individual studies in order to address specific research questions, resulting in the representation of a limited number of species and local levels of call variation (MacSwiney et al. 2008). Moreover, the material arising from these individual efforts is seldom shared or stored in public repositories. Considering the great call variation that exists even within the same species, this shortage or lack of accessibility to reference material has impeded the implementation of acoustic studies of entire bat communities or extended geographic regions (Walters et al. 2013).

The first public repository of bat acoustic material dated from the 1960s and was held by the British Library (Table 3.1). However, it was not a specialized acoustic bat library and most of the material was recorded opportunistically without supporting information (e.g. release type, recording habitat, and recording equipment). The pioneering work of Novick (1977) on the compilation of bat echolocation calls summarizes the efforts of many scientists to collect recordings and describe echolocation calls for more than 130 species from several tropical countries. Almost two decades had to pass for the first specialized bat acoustic libraries to appear in Australia and the United States, but still with clear limitations: (a) most of the information can only be accessed online; (b) recordings lack proper metadata and; (c) some of the websites are unmaintained. At the beginning of the following decade, several bat echolocation books and guides were published at the local and national level, producing the first acoustic characterization of bats from a megadiverse region (Madagascar) (Bennett and Russ 2001). These initial efforts were important because they described bat call diversity at broader scales, but they did not address the problem of data availability for more advanced call analyses, as most were disseminated in printed versions only. Up to the end of the 2010s, information pertaining to standard call parameters (e.g. maximum frequency, call duration, minimum frequency) could only be acquired from the literature since WAV files were not public, restraining more in depth acoustic analysis and additional measurements of calls.

The creation of Echobank (Collen 2012) has been a major leap forward in bat acoustic repositories. With a total of 53,488 calls in 3531 call sequences from 297 species, 94 genera and 18 families, this library is currently hosted at the Centre for Biodiversity and Environment Research (CBER), University College London. This repository is composed by full spectrum, time expanded and real time calls donated by a consortium of scientists using a variety of different recording equipment and methods from many different habitats and countries (Walters et al. 2013). Due to its currently unmatched coverage of European species, Echobank will likely be essential for the creation of automatic classifiers capable of analyzing data coming from “iBats”, one of the biggest European bat acoustic monitoring programs (Jones

Table 3.1 Efforts worldwide that contributed to bat acoustic repositories

Year	Name	Type	No. species	No. records	Recording type	Country	Reference
N/A	BatCalls.org*	Library	42	91	Time expansion	United States	http://www.batcalls.org
N/A	Bat conservation trust sound library	Library	15	27	Heterodyne	Great Britain	http://www.bats.org.uk
N/A	Cornell lab of ornithology-Macaulay library	Library	29	258	Time expansion	Worldwide	http://www.macaulaylibrary.org
N/A	Pacific northwest bat call library	Library	10	33	Frequency division	United States	http://www.depts.washington.edu/sdwasm/pnwbat/batcall.html
N/A	Wyoming bat call library	Library	14	73	Frequency division	United States	https://www.uwyo.edu/wyndd/data-dissemination/priority-data-comp/wyoming-bat-call-library/
1997	BatCall-Museum of Southwestern Biology*	Library	22	3821	Frequency division	United States	http://www.msb.unm.edu/mammals / http://www.msb.unm.edu/mammals/knlknl
1969	British library-British sound archive	Library	139	700	Time expansion	Europe	http://www.bl.uk/soundarchive
1996	Southeastern Australian bat call library*	Library	9	31	Frequency division	Australia	http://www.csu.edu.au/batcall/batcall1.html
2001	Key to the bat calls of south-east Queensland and north-east New South Wales	Key/guide	29	NA	Zero-crossing	Australia	Reinhold et al. (2001)
2001	The bats of Madagascar: an identification guide with descriptions of echolocation calls	Key/guide	18	NA	Time expansion	Madagascar	Bennett and Russ (2001)
2009	Avisoft bioacoustics	Library	26	62	Time expansion	Europe	http://www.batcalls.com
2012	British bat calls: A guide to calls, sound analysis and species identification	Key/guide				Great Britain	Russ (2012)

2012	Chave de identificação de vocalizações dos morcegos de Portugal continental	Key/ guide	22	NA	Real time	Portugal	Rainho et al. (2012)
2012	EchoBank	Library	297	3531	Time expansion and real time	Worldwide	Collen (2012)
2014	Social calls of the bats of Britain and Ireland	Key/ guide	23	136	Real time	Britain, Ireland	www.pelagicpublishing.com/social-calls-library.html
2016	Acoustic identification of Mexican bats based on taxonomic and ecological constraints on call design	Library	95	2327	Real time	Mexico	Zamora-Gutierrez et al. (2016)
2016	MORCEGOTECA: biblioteca virtual de ultrassons de morcegos	Library	15	18	Real time	Brasil	https://ppbio.inpa.gov.br/en/Bat_Library
2017	Acoustic call library and detection distances for bats of Swaziland	Library	20	145	Zero-crossing	South Africa	Monadjem et al. (2017)
2017	Identification guide to bat echolocation calls of Solomon Islands and Bougainville	Key/ guide	16	NA	Real time	Solomon Islands	http://ausbats.org.au/bat-calls-of-solomon-islands/4593992119
2018	Nepal bat call library	Library	15	NA	Real time	Nepal	http://smcrf.org/resource/nepalbatcall/
2018	Sonozotz	Library	69	1960	Real time	Mexico	Soon through the CONABIO portal

The libraries with an asterisk have broken internet links and their information was extracted and modified from Walters et al. (2013)

et al. 2013; Walters et al. 2013). Nevertheless, tropical bats remain underrepresented in Echobank and information is only available upon direct request (Walters et al. 2013).

A few years later, a group of Mexican bat researchers presented at the 2018 NASBR meeting the first reference acoustic library of Mexican Nearctic and Neotropical insectivorous bats “Sonozotz-AMMAC-CONABIO”, which is the first major effort for a bat acoustic library in a Neotropical megadiverse country. Sonozotz was assembled following a standardized sampling and recording protocol aiming to capture as much intra and interspecific call variation as possible from Mexican insectivorous bats. Having a standardized data gathering protocol offers the opportunity to extrapolate experience and expertise for the creation of reference call libraries in other countries. The geographic extent of this dataset includes eight Mexican ecoregions ranging from sea level up to 3600 masl. Represented habitats encompass a diverse collection of ecosystems, from the northern xerophytic scrublands to the southern Mexican tropical forests. A total of 1664 individuals belonging to 7 families and 69 species were recorded, which corresponds to 64% of the insectivorous bat species occurring in Mexico (Zamora-Gutierrez et al. 2020). Although the recordings for this project were collected following standardized protocols, sampling methods were designed to avoid biases towards any particular method or microhabitat. Sonozotz recordings will be freely available in WAV format, together with their associated metadata, through the National Commission for the Knowledge and Use of Biodiversity (CONABIO). Once online, it will be possible to add new recordings, following a curatorial process to ensure data quality and reliability.

The creation and hosting of an acoustic library poses several challenges that could explain their scarcity. Acoustic files are large and thus demand copious storage space, sufficient internet connectivity and considerable computational power for proper data management. If a library is open for new contributions, curators or a group of experts are necessary in order to maintain quality control of incoming recordings and annotations, which can be time consuming and/or expensive. It is also important to have a system that controls information flux in order to adequately document data access. Another barrier can be the willingness to share data, but the trend of making datasets available via online systems, such as Dryad, is becoming the norm.

3.5 Beyond Single Species Classification

The advances made in the field of bat acoustics in the last decade have contributed to an engagement in novel research fields. However, the acoustic identification of some bat groups to the species level remains a challenge (Walters et al. 2013). Researchers are beginning to realize that we might need to change the focus of acoustic research to other taxonomic levels. For example, Zamora-Gutierrez et al. (2016) applied hierarchical random forest techniques to the classification of 59 species at different taxonomic and ecological levels, and found that the use of broader classification groups (e.g. guilds) yielded improved classification accuracy when compared to the use of species. Call identification based on the ecological characteristics of the species could be used to rapidly characterize ensemble/environment associations or to track changes in community structure, and could even help to reduce the costs of monitoring tropical bat communities, which is a crucial challenge given the limited funding these regions often devote to conservation efforts (Zamora-Gutierrez et al. 2016).

The ecological information contained in bat calls reflect the functional diversity of the studied system and can provide important clues to the ecological processes and the subsequent ecosystem services that are maintained or lost in the environment (Cadotte et al. 2011; Jones et al. 2013). A new perspective on the use of acoustic data is arising, in which species traits, such as body size, can potentially be inferred from call characteristics (Penone et al. 2018). In this context, calls without species ID produced by monitoring programs or citizen science projects could be used to explore biological patterns at various spatial and temporal scales (Penone et al. 2018). The inference of traits from call characteristics could also be useful for exploring purely ecological questions or conservation concerns, such as species vulnerability to global change.

Improvements in data management, analysis automation and access to low-cost ultrasonic detectors have allowed the establishment of community and citizen science monitoring programs at large spatial and temporal scales. One of the largest acoustic surveys worldwide is iBats (http://www.ibats.co.uk) (Jones et al. 2013), presented at the 2007 NASBR meeting. This monitoring program is carried out by a group of volunteers driving car transects across Europe and other parts of the world. iBats has gathered an incredible amount of data over a decade that now, thanks to the development of the automatic European bat calls ID tool (Walters et al. 2012) and the creation of Bat Detective (Mac Aodha et al. 2018), can be analyzed in order to disentangle the patterns and trends in the bat communities of almost an entire continent. Likewise, the North American Bat Monitoring Program (NABat), introduced at the 2012 NASBR meeting, was created to monitor bats across America (Loeb et al. 2015). NABat monitoring strategy includes different types of acoustic monitoring methods (stationary vs. mobile) as well as other relevant ecological assessments, such as roost counts.

Acoustic surveys have provided important insights into the effects of anthropogenic activities on bat activity and diversity (Voigt and Kingston 2016), helping to improve our understanding of current important threats to bats worldwide (i.e. wind farms, white nose syndrome). Insights on how human activities affect biodiversity are a crucial prerequisite for the development and application of effective species conservation programs. Bats are important indicators of biodiversity trends (Jones et al. 2009) and acoustic surveys are a cost-effective and efficient method offering the opportunity to monitor bats consistently through time from regional to global scales.

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Chapter 4

How Noise Affects Bats and What It Reveals About Their Biosonar Systems

Michael S. Smotherman, Andrea Megela Simmons, and James A. Simmons

Abstract Echolocating bats use sounds for both perceiving their surroundings and social communication, which makes bats vulnerable to environmental and anthropogenic noise. Whether a particular noise source affects bats depends upon the acoustic properties of the noise and those of the bat's pulses as well as whether the bat is roosting, commuting or foraging. This chapter reviews some of the key discoveries on this topic that have emerged since the first North American Society of Bat Research (NASBR) meeting 50 years ago. A variety of different experimental approaches focused on noise have synergistically advanced the study of bat biosonar and acoustic communication. Psychoacoustic studies used noise stimuli to probe mechanistic questions about how the bat's brain processes and interprets echoes. Behavioral studies examined the long-term effects of intense noise on bat hearing, revealing that bats were surprisingly resistant to noise-induced hearing deficits at noise levels that cause hearing loss in other mammals. Lab and field studies have explored how bats respond to noise, focusing especially on behaviors that appear to successfully mitigate its negative effects. Field research has investigated the ecological consequences of both natural and anthropogenic noise, identifying the significant threats of noise pollution for bat populations. Collectively, these studies provide a cohesive framework for understanding the evolution of bat biosonar while also identifying key issues for ensuring their conservation.

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4.1 Why Study How Noise Affects Bats?

Echolocating bats broadcast high-frequency sounds and rely upon a continuous stream of returning echoes to create and maintain an internal perceptual representation of their surroundings (Griffin 1958). Following its discovery, research about echolocation has encompassed a wide variety of acoustic, behavioral, and neural aspects of this active mode of perception (Fenton et al. 2016; Neuweiler 2000; Surlykke et al. 2014). Bats produce intense (100–140 dB SPL) sonar pulses, while the echoes they receive are less intense (0–80 dB SPL) and vary in strength according to the size and distance of objects (Stilz and Schnitzler 2012).

The informative cues embedded in even strong returning echoes may be distorted and masked by environmental noise. Environmental noise can come from many sources, such as wind, water, insects, other bats, and, increasingly, from anthropogenic sources. Because bats rely on their sense of hearing to orient, navigate, and forage, they have likely evolved behavioral and physiological mechanisms to counteract the adverse effects of noise on echolocation. This makes it generally interesting to study how bats perform under noisy conditions, and many studies have investigated the behavioral strategies used to compensate for noise effects.

Noise, defined broadly as irrelevant signals occurring at some time point with respect to the signal of interest, has long been used as a tool to study the psychophysics and physiology of hearing. Much of our understanding of human hearing is based on masking experiments that ask listeners to detect particular signals occurring during (simultaneous masking), before (backward masking), or after (forward masking) exposure to noise. Because irrelevant signals can occur unpredictably both in time and in space, detecting biologically meaningful signals in a noisy world is a challenge for all animals. Consequently, both senders and receivers have evolved strategies and mechanisms to improve signal transmission. This question has broad relevance because it gets to the heart of how the nervous system is organized to conduct a specialized suite of rapid and sophisticated calculations.

Bat biosonar offers a valuable opportunity for studying impacts of noise on signaling because echolocating animals are both sender and receiver. The physical properties of the acoustic signal have special relevance for biosonar (detection range and acuity) and their ecological consequences can be evaluated based upon mathematical predictions. In this chapter, we briefly review the acute and chronic effects of noise on echolocation and hearing in bats, and take a close look at how noise impacts the detection, discrimination, and localization of targets. We discuss how bats behave in the presence of noise, and review evidence that bats actively manipulate their biosonar pulses to mitigate the impact of noise. We then explore how environmental and anthropogenic noise may influence some important aspects of their daily lives and their long-term conservation. Lastly, we conclude with a discussion of important questions yet to be answered.

4.2 Noise Jamming Experiments Reveal the Extraordinary Precision of Bat Sonar

Early work on echolocation (Griffin 1958; Grinnell et al. 2016) occurred contemporaneously with the development of radar and sonar systems during World War II. Noise experiments were conducted to assess how jamming signals interfere with the registering of targets, and to measure the minimal signal-to-noise ratio (SNR) needed for detection of weak echoes in noise. SNR is an important index of the efficiency with which information in echoes is used by manmade receivers (Woodward 1953).

Initial experiments (Griffin 1958; Griffin and Grinnell 1958) used obstacle avoidance tests in which bats were flown past rows of thin vertical wires to establish whether their hearing was sensitive enough to detect the wires in time to avoid collisions. Then, the flying bat was exposed to noise to determine how much noise was needed to prevent detection of the wires and induce collisions (Griffin et al. 1963). The technical problems in these experiments were daunting. First, the species being studied, the little brown bat (*Myotis lucifugus*), transmits sounds at such high levels that it was unlikely the noise could be made intense enough to jam the echoes from the wires, which would themselves be surprisingly strong due to the reflective nature of the wires. So, a different species of bat was examined, Townsend's big-eared bat (*Plecotus townsendii*), which was known to emit weaker biosonar sounds. The resulting echoes from the wires would be correspondingly weaker and easier to jam with noise. Second, because the bat is in flight, its location in the room as it approaches and then detects the wires varies, making it difficult to specify the strength of the noise in relation to the echoes at the point where the bat's initial reaction occurs. To ensure that the echoes really were blanketed by the noise, an array of specially-built ultrasonic loudspeakers were positioned on the far wall to project a relatively uniform level of noise that filled the likely space where the bat might pass as it approached the wires (Griffin et al. 1963).

The initial finding from these experiments was that the bats could detect echoes at a SNR of about −10 dB (the target echo was 10 dB quieter than the noise). By signal detection theory, however, the target echo strength should be greater than the noise (by at least +1 dB) for threshold detection (Griffin and Grinnell 1958; Griffin et al. 1963). But bats receive echoes from two ears, not just one, and the ears are pointed in different directions while the bat approaches the wires at an oblique angle with its head aimed at them. The acoustic consequences of having the ears aimed to the left and right while the nearest wire is straight ahead are that echoes from the wires arrive at both ears with similar strengths, while the noise radiated from the loudspeakers is stronger at the ear facing them than at the ear facing away (Grinnell 1963a, b). The difference in noise levels at the two ears partially unmasks the echoes, in a phenomenon now known as the binaural masking level difference. The advantage thus gained increases the echo SNR above 0 dB, up to +10 dB, above threshold detection.

Obstacle avoidance and target discrimination may require different levels of acuity and might therefore be differentially sensitive to noise interference. Research on the ability of bats to discriminate between objects differing in shape began in the former Soviet Union (Airapet'yants and Konstantinov 1973). In these experiments, lesser mouse-eared bats (*Myotis oxygnathus*) were trained to fly towards one of three different solid objects—a cube, a cone, and a cylinder suspended by a thin wire, with dimensions of 15–30 cm. The correct object had a built-in feeding tray with mealworms to reward the bat for landing on it. After the bats learned to find the correct target by identifying its echoes, a field of intense noise was delivered by an array of ultrasonic loudspeakers that filled the flight space with a uniform noise level, similar to the array described above. The bats easily learned the discrimination task in the quiet, and they were able to continue their performance in the noise by increasing the sound pressure and duration of their broadcasts so that the echoes were kept above the noise (Airapet'yants and Konstantinov 1973). A similar reaction had been recorded in the wire avoidance experiments described above: bats emitted stronger sounds in the presence of noise as an adaptation to resist the effects of the jamming sound.

An alternative procedure for assessing target discrimination abilities was introduced at the 1973 NASBR meeting in New Orleans (Simmons 1973a): it involved training bats to sit on a small, elevated platform and detect or discriminate between objects placed in front of it using their echolocation (Simmons 1973b). Once the bat has successfully learned to perform this simplified type of task, noise can be delivered from one or two ultrasonic loudspeakers to jam the echoes (Simmons 2017). Here, the volume of space occupied by the bat that has to be filled with noise is very small, only a few centimeters in dimensions. Furthermore, the ability to place the loudspeaker(s) close to the bat on the platform provides for much more intense jamming noise. A variation on this approach is the delay discrimination experiment, such as those performed with big brown bats (*Eptesicus fuscus*) by Masters and Raver (1996) and Simmons (2017). In these experiments, a new, "virtual reality" stimulus was introduced: The bat's echolocation calls were picked up by microphones, the resulting electrical signals were electronically delayed, and then artificial echoes were created by feeding the delayed signals to small ultrasonic loudspeakers that played the sounds back to the bat. This process produced electronically-generated echoes that simulated the presence of actual objects (Simmons 1973b). Echo detection or delay discrimination was assessed by manipulating the electronic signals instead of moving physical objects.

To understand how well bats can discriminate targets (and how that capacity is impacted by noise), it is essential to know how well bats can resolve very fine differences in target distance. With flying bats, there are too many uncontrollable variables to make precise measurements, but with stationary bats performing the two-choice behavioral assay it became possible to evaluate sonar performance under much more controlled conditions. Still, the two-choice assay has some limitations. The first such tests yielded relatively low distance discrimination acuity, in the range of 1–2 cm, or 50–100 μs of echo delay times; the poor performance was ascribed to the bat's movements on the platform while emitting echolocation sounds even though the loudspeaker delivering electronically delayed echoes remained stationary, which confounded the bat's distance perception (Simmons 2017).

Information theory (Woodward 1953) can predict the delay discrimination performance that an “ideal receiver” ought to achieve at a specified SNR. For bats, delay discrimination performance in the 50–100 μs region is possible at SNR as low as 11–15 dB SPL, only slightly larger than the level required for detection (Griffin et al. 1963). To use the two-choice delay discrimination method for estimating the jamming effects of noise, the size of the delay difference to be discriminated should be even larger than the 50–100 μs limit imposed by the two-choice method. The SNR needed to jam the bat’s performance at 232 μs was 8–10 dB SPL, which is approximately what information theory predicts (Simmons 2017).

At higher echo SNRs, information theory predicts much smaller delay-discrimination acuity in the range of fractions of a microsecond (Sanderson et al. 2003). This fine degree of delay accuracy is beyond the reach of the ordinary two-choice echo-delay discrimination method. To extend delay acuity measurements down to the much smaller time differences required to assess the relevance of the theory to bat echolocation, a new stimulus presentation process was developed that could get around the problem of the bat’s movements on the platform. Instead of training bats to discriminate electronic echo delay between two separate virtual targets (Simmons 1973b), bats were trained to perceive electronic echoes from a single source that sequentially alternated in delay from one broadcast to the next (Simmons et al. 1990). By alternating or jittering the echo delay, the bat’s movements on the platform were largely negated. At an echo SNR of 36 dB, discrimination was about 0.05 μs, which is approximately what information theory predicts (Sanderson et al. 2003). Figure 4.1 plots the results from the echo jitter experiments in relation to the performance of an ideal receiver. Such fine sensitivity to changes in echo delay is astonishing, yet control tests confirm that it is due to auditory registration of the jittering echo delays, not a spectral artifact of the experimental set-up (Simmons 1993). The origin of such delay hyperacuity most likely is the auditory system’s use of a time-frequency, or spectrogram-like, representation for biosonar broadcasts and echoes (Sanderson et al. 2003). The take-home message here is that through a combination of evolving behavioral assays and the application of information theory, background noise proved to be a critical tool for elucidating the amazing capabilities of echolocating bats to discriminate fine features of their targets. The neural or mechanistic basis for this ability remains unknown and may only exist in bats and cetaceans. This also highlights the fact that even moderate levels of noise are likely to impede a bat’s ability to discriminate targets and obstacles without necessarily negating their ability to detect and localize them.

4.3 Bats Are Remarkably Resilient to Noise in the Lab

Psychophysical and laboratory flight experiments show that big brown bats are behaviorally resistant to noise exposures that in other vertebrate species would produce temporary hearing losses. In psychophysical experiments, bats’ thresholds to frequency-modulated (FM) sweeps similar to their biosonar pulses were measured

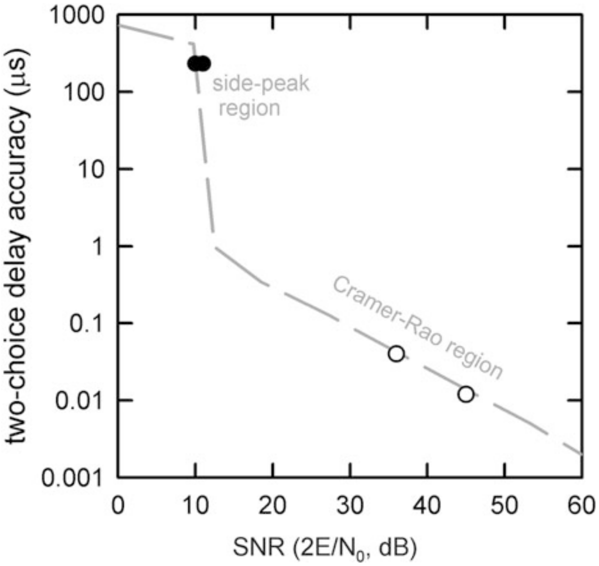


Fig. 4.1 Expected performance for accurate discrimination of echo delay (y axis) if the bat uses an ideal receiver, which stores a replica of each broadcast and then compares it to a similar representation of each echo to produce an estimate of the echo's delay (cross-correlation; Woodward 1953). The *solid black* data points plot the signal-to-noise ratio (SNR) of echoes at the condition where big brown bats fail to discriminate delay differences of 116 or 232 µs (Simmons 2017). The open circles plot the condition where big brown bats fail to detect much smaller changes in echo delay presented as jitter in delay (Simmons et al. 1990). The ideal receiver curve is divided into a Cramer-Rao region, where performance is inversely related to echo SNR, and a region where performance deteriorates more steeply due to the effects of intense noise on recognition of the shape of the ideal receiver's output (Sanderson et al. 2003)

before and after one-hour-long exposures to wideband (10–100 kHz) or band-limited (bandwidths of 10–50 kHz) noise at sound pressure levels of 116 dB SPL. Thresholds at 2, 5, and 20 min post-exposure did not differ from those prior to exposure (Simmons et al. 2016, 2017), suggesting that no hearing loss due to these intense noise exposures occurred. By contrast, other terrestrial mammals tested under similar experimental conditions experience significant increases in detection thresholds lasting up to several hours or even days after noise exposure. Bats' ability to fly through a narrow corridor surrounded by interfering obstacles remained intact at 2 and 5 min after noise exposures at levels up to 123 dB SPL (Hom et al. 2016; Simmons et al. 2018). Biosonar pulse emissions did not differ in temporal structure before and after noise exposure, indicating that the bats did not perceive the flight task as more difficult after exposure. Because the natural soundscape of echolocating bats can include aggregate sound pressure levels as intense as 100–140 dB SPL, these data suggest that bats have evolved mechanisms to resist the interfering effects of prior noise exposures (forward masking). These results extend findings that simultaneous noise presentation also does not interfere with echolocation (Luo et al. 2015a).

4.4 Does Environmental Noise Influence Bat Behavior in Nature?

Environmental noise impacts communication by decreasing the SNR at the receiver, making it more challenging for animals, including bats, to detect, localize, and classify biologically-meaningful sounds. Sources of abiotic noise that affect communication in other animals, such as wind passing over vegetation or flowing water, fall well below the ultrasonic range of frequencies used by most bats (Brumm and Slabbekoorn 2005). The energy spectra of anthropogenic noise sources, such as from machinery, also are concentrated at lower frequencies (<30 kHz) than the echolocation calls of many species. In addition, due to atmospheric attenuation, the higher frequency components of noise attenuate more quickly than lower frequency components, so that these high frequencies do not propagate far from their sources. Nonetheless, there is evidence that echolocating bats actively avoid both abiotic and anthropogenic noise. On the other hand, there are many notable examples of bats roosting, mating, and foraging in dense urban habitats, suggesting that the impact of anthropogenic noise can vary across species, depending upon the acoustic characteristics of their echolocation calls, their preferred prey, and their foraging styles.

Bunkley et al. (2015) conducted passive acoustic surveys of activity of several bat species at gas wells with and without compressor noise. One species, the Mexican free-tailed bat (*Tadarida brasiliensis*), showed a large decrease in activity at noisy compared to quiet wells, while activity levels of four other species (*M. lucifugus*, *Myotis californicus*, *Myotis ciliolabrum*, and *Parastrellus hesperus*) did not vary between sites. Compressor noise contains energy up to 24 kHz and the echolocation calls of the Mexican free-tailed bat contain energy below 35 kHz; the four species whose foraging were not affected by the compressor noise all emitted echolocation calls with frequencies >35 kHz. It is important to note that in the presence of compressor noise, Mexican free-tailed bats decreased call bandwidth, thus increasing SNR, and increased call duration.

Several echolocating species (e.g. little brown bats, big brown bats, and Daubenton's bat (*Myotis daubentonii*)) forage over streams, and seem to prefer calm (quieter) over turbulent (more noisy) waters, even though turbulent waters may support higher insect density (Mackey and Barclay 1989; Rydell et al. 1999). In these experiments, playbacks of sounds of turbulent waters to bats foraging over calm waters reduced their foraging activity. These results suggest that either playbacks masked the low intensity echoes reflected from small insect prey, or bats found the noise to be aversive. The greater mouse-eared bat (*Myotis myotis*) is a gleaning bat that finds prey by passively listening to the rustling sounds made by these prey as they move through their habitat. Schaub et al. (2008) showed that these gleaners avoid foraging areas with high levels of background noise, and that vegetation noise (e.g. wind rustling leaves) produced more avoidance behaviors than traffic noise, even if traffic noise was more intense. Vegetation noise has a similar spectrum as prey-generated noise, thus accounting for its greater impact on foraging. The authors also noted that the bats' ability to fly and maneuver were not obviously impaired in the presence of noise, suggesting that echolocation itself remained intact.

Aside from an explanation based on masking, bat avoidance of noisy environments may be due to an aversive effect of the noise. Luo et al. (2015b) quantified foraging behavior of Daubenton's bats under conditions of background clutter and playbacks of traffic noise. The echolocation calls of Daubenton's bats do not overlap spectrally with traffic noise, but both overlapping and non-overlapping traffic noise decreased the total number of foraging flights. Still, the number of flights required to capture prey successfully was similar in control and in noise conditions. The authors concluded that the traffic noise was aversive to the bats but did not interfere with their echolocation.

Several species of bats alter their commuting routes to avoid busy roads (Bennett and Zurcher 2013). This avoidance behavior increased in landscapes where tree lines and canopies were absent (and thus could not provide visual-spatial cues), as well as with levels of traffic noise. These results do not distinguish between an explanation based on noise masking or on noise aversion. Whatever the mechanism, roads can serve as barriers to finding prey and roosting sites.

Collectively, these studies provide ample evidence that both foraging and commuting bats are sensitive to background noise. The amount of spectral overlap between the noise and pulse acoustics is a central factor mediating these effects. The psychophysical studies from Sect. 4.2 above demonstrate that even modest noise levels can sharply degrade a bat's ability to discriminate fine details, which may drive bats from an area because the noise makes foraging less efficient. However, bats have adaptations for improving their echolocation in noise and can endure under surprisingly noisy conditions if necessary. So, an important unresolved issue is whether bats are truly repelled by any type of naturally occurring or anthropogenic noises, and if so why. This has important implications for conservation efforts because of the interest in using noise as a deterrent around wind turbines or in places where bats roost in buildings or archeological sites.

4.5 Do Echolocating Bats Interfere with Each Other?

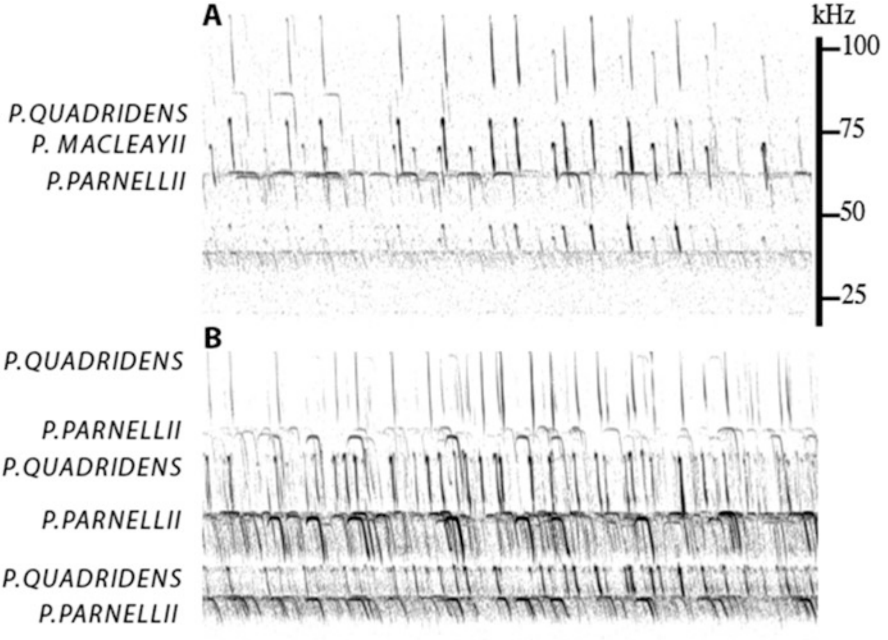
Bats must also contend with acoustic interference from other bats. Acoustic interference has influenced the evolution of echolocation in ways that allow closely-related bats to share microhabitats such as caves. Kingston et al. (2001) reported evidence of acoustic divergence in echolocation pulses amongst two cryptic species of Malaysian *Hipposideros* bats. In this example, there were two overlapping populations of the bicolored leaf-nosed bat (*Hipposideros bicolor*), a constant-frequency (CF) bat that exhibited distinct differences in pulse CF (131 kHz and

142 kHz) within the population, despite foraging in overlapping habitat for similar prey. This difference in CF between the two populations appeared inconsistent with the acoustic resource partitioning hypothesis, which predicts a correlation between pulse frequency and preferred prey size. Instead, the divergence in pulse frequencies may arise from the need for separate social communication channels. A narrowly tuned acoustic fovea is an essential feature of the ear of high-duty cycle CF bats, and presumably they would not be able to effectively change the frequency of their social calls without simultaneously shifting the bandwidth of their acoustic fovea; thus, sonar pulse bandwidth would need to change in concert with social calls so that both remained in line with the acoustic fovea. Since social calls can influence reproductive success, this mechanism can potentially facilitate rapid evolutionary changes in pulse acoustics due to sensory drive.

Similar patterns of socially-driven acoustic divergence have also been documented in the neotropical mustached bat, *Pteronotus parnellii*, which is now considered to be a group of cryptic species distinguishable by genetic differences and slight variations in the frequency of their CF component across their geographic range (Clare et al. 2013). The *Pteronotus* species are members of the family Mormoopidae, many of which are obligate cave roosters. Caves are a limited resource, and are typically shared by several different Mormoopidae (*Pteronotus* and *Mormoops* spp.) where they co-occur. Although *P. parnellii* is considered a true CF bat because of its comparatively long CF component (~20 ms), there are at least 15 other *Pteronotus* species whose echolocation calls appear to have a short (>1–2 ms) initial CF component followed by a 10–15 kHz downward FM sweep. Like *P. parnellii*, all of these species principally rely upon a dominant second harmonic but are capable of accentuating additional harmonic components under noisy or cluttered conditions (Smotherman and Guillen-Servent 2008).

Caves housing many Mormoopidae species offer an interesting opportunity to explore whether different species display evidence of acoustic divergence due to interspecific interference. Similar assemblages of Mormoopidae species are found throughout Mexico, Central and South America and the Greater Antilles. One of the most striking acoustic features of these groups is the distribution of frequency characteristics amongst species that share caves (Fig. 4.2). Individual species within a given cave vary considerably in their morphological characteristics, foraging styles, and preferred prey, which in turn undoubtedly accounts for some of the differences in pulse acoustics. But, as in the case of *Hipposideros bicolor*, the differences may also reflect social interactions within the cave. For example, it is possible that dense populations of mustached bats, with their high intensity, high duty-cycle pulses, could prohibit or delay other species from exiting the cave at the same time unless that species uses a distinctly different sonar bandwidth. Both inter- and intraspecific competition favors bats that can exit the cave sooner rather than later than their competitors. If one species of bat cannot navigate the cave due to high levels of acoustic interference from another species, then selective pressures could drive pulse bandwidths towards nearby open channels.

Early during an emergence, solitary mustached bats exiting the cave emit predominantly single (second) harmonic pulses, similar to what they use while foraging



C

JAMAICA		MEXICO	
Species	*Peak frequency*	*Species*	*Peak frequency*
P. parnellii	61 kHz	*P. parnellii*	65 kHz
P. macleayii	70 kHz	*P. davyi*	74 kHz
P. quadridens	80 kHz	*P. personatus*	85 kHz
M. blainvillii	52 kHz	*M. megalophylla*	55 kHz

Fig. 4.2 Spectrograms of bat pulses recorded at the mouth of Windsor Cave, Jamaica, during early evening emergence. Four different species of Mormoopidae share this cave and exit together during overlapping time windows. In (**a**), the sonar pulses of *Pteronotus parnellii*, *Pteronotos macleayii* and *Pteronotus quadridens* are overlapping in time but are spectrally segregated based on the beginning peak frequencies. The acoustic segregation is especially evident in (**b**), where the two most abundant species almost completely fill the spectrum with their tightly interleaving multi-harmonic pulses. (**c**) Comparing pulse peak frequencies (initial CF component) of species assemblages in Jamaica's Windsor cave versus one located in central Mexico (Xalapa) supports the hypothesis that spectral spacing to minimize interference may be necessary for closely related species that are obliged to share caves. In Mexico, *P. parnellii* is now known as *P. mesoamericanus*

alone in an open space. When small numbers of bats are exiting the cave, acoustic overlap between individuals is rare (Fig. 4.2a), but as the density of bats leaving the cave increases and noise levels elevate, the bats begin emphasizing the lower and upper harmonic components of their pulses (Fig. 4.2b), indicating that they are experiencing interference. Adding additional harmonics improves signal detection and ranging in noisy conditions, but also inevitably makes the noise conditions even worse for the group. Remarkably, the bats are for the most part still able to minimize spectral overlap by tightly interweaving the harmonic structure of their pulses. A telling sign that species may indeed be impacting each other emerges when one compares the peak CF frequencies of assemblages of bats sharing a cave in Jamaica versus a complimentary group of species sharing a cave in central Mexico; the CF frequencies of entire species assemblages appear to shift in parallel (Fig. 4.2c). Acoustic resource partitioning could account for the parallel changes in pulse frequencies across the assemblage, but it seems unlikely that all four species would undergo the same shift due to changes in prey size. Instead, the need to minimize acoustic interference between species that obligatorily share caves offers a simpler explanation. Only one of the four Moormopidae species in each cave, *P. parnellii* complex, relies upon an acoustic fovea (Kossl et al. 1999), and this species produces the loudest and longest calls. An alternate possibility might be that changes in *P. parnellii*'s pulse frequency subsequently triggered a cascade of compensatory frequency shifts across the assemblage of sympatric species sharing the caves.

Additional evidence that foraging bats suffer impaired prey detection capabilities in the presence of other bats comes from on-board recordings of pulses emitted by flying, foraging bats (Cvikel et al. 2015). Using a miniature head-mounted microphone and GPS recording system, it was discovered that foraging bats aggregated to improve the odds of finding patches of prey. But at higher group densities the foraging success of individuals was compromised by the presence of conspecifics. The interference didn't arise from conspecific pulse emissions (i.e. acoustic interference), but rather from the need to redirect attention to nearby bats which became obstacles (i.e. attentional interference). In practice, it may be difficult to disentangle the relative effects of acoustic versus attentional interference in biosonar. FM bats approaching a target or encountering an obstacle typically shorten pulse duration and increase bandwidth, which is often accompanied by a slight elevation in terminal frequency. Shifts in pulse terminal frequency in the presence of other bats have been interpreted as evidence of a jamming avoidance response intended to enhance spectral separation between conspecifics (Gillam et al. 2007; Ulanovsky et al. 2004). But as Cvikel et al. (2015) illustrated, it is challenging to disentangle the precise motivations for why bats change specific acoustic features of their pulses in every situation.

4.6 Do Bats Perform a Jamming Avoidance Response?

Since bats are especially sensitive to jamming interference by noises that overlap with their own pulses, the most confounding source of interference should be the pulse emissions of other nearby bats, and especially conspecifics. In theory, this should be problematic for any bats that roost or fly in large social groups, and yet there is surprisingly little evidence that bats suffer degraded sonar performance in the presence of other bats. Either bats possess mechanisms for excluding or ignoring the sounds of other bats or they employ some compensatory behavioral strategies for echolocating in the presence of other bats. Either or both may be necessary depending on the roosting and foraging ecologies of different species, environmental conditions, and behavioral context.

Bats impacted by noise may be best served by simply leaving the area, but roosting sites, watering holes, and food patches are shared resources where bats may benefit by being able to continue echolocating in the presence of other bats. The ability to manipulate their own vocalizations to minimize mutual interference would allow bats to exploit or at least compete for a resource without having to disengage, change trajectory, or leave the area. The first evidence that bats performed any sort of vocal jamming avoidance response was obtained from one of the most highly gregarious species of bats, the European free-tailed bat (*Tadarida teniotis*) (Ulanovsky et al. 2004). Members of the *Tadarida* genus use relatively long (up to 25 ms) and shallow (quasi-constant frequency) FM sweeps when commuting in open space, although they quickly revert to short multi-harmonic broadband pulses in cluttered spaces. Ulanovsky et al. (2004) reported that pairs of bats shifted the frequencies of their pulses in concert to increase spectral separation when sharing the same air space. Notably, however, field recordings from the Egyptian tomb bat, *Taphozous perforates*, did not identify any jamming avoidance response. Gillam et al. (2007) presented artificial playbacks of echolocation pulses to passing Mexican free-tailed bats in the field, and showed that these bats shifted their pulse frequencies within 200 ms of playback onset. These frequency shifts were correlated with the initial amount of spectral overlap between the bats' pulses and the playback stimuli.

Evidence in support of a spectral jamming avoidance response has also been obtained in the lab. Stationary big brown bats either raised or lowered the terminal frequency of their FM sweeps in response to a jamming tone presented during a two-alternative forced choice experiment that depended on the use of echolocation (Bates et al. 2008). Captive Mexican free-tailed bats flying in the lab emit short broadband pulses but were still found to shift the frequency parameters of their pulses upwards in response to a continuous noise stimulus that overlapped with at least part of their pulses Tressler and Smotherman 2009). In another elegant experiment using on-board microphones it was found that small groups of Eastern bent-wing bats (*Miniopterus fuliginosus*) flying together in a confined space dynamically shifted the terminal frequencies of their pulses as they passed one another (Hase et al. 2016, 2018).

The above examples support the idea that at least some bats readily perform some form of jamming avoidance, but it is also apparent that some species do not (Gotze et al. 2016). Of some concern when interpreting the above data is that FM bats rarely change an isolated acoustic parameter of their pulses. The most generic vocal response to noise exhibited by all mammals is to simply call louder—the so-called Lombard response (Lombard 1911). Biomechanical constraints of the vertebrate larynx and respiratory-laryngeal reflexes typically cause any increase in loudness to be accompanied by a change in fundamental frequency and bandwidth (Smotherman 2007, p. 63; Kobayasi et al. 2012, p. 65). Horseshoe bats can independently alter frequency and intensity parameters in response to different acoustic cues (Hage et al. 2013), which may be an adaptation for Doppler-shift compensation behavior. The same cannot be said, however, for FM bats. When Mexican free-tailed bats shift their pulse frequency away from an interfering tone, they also change pulse intensity and duration. Changing intensity and duration are common mechanisms for improving signal detection in noise, which raises the possibility that any observed changes in frequency might be secondary to changes in intensity or duration (Tressler et al. 2011). This confounding explanation must be discounted, however, because both Mexican free-tailed bats and big brown bats were sometimes observed to lower pulse frequencies in the presence of other bats or overlapping acoustic stimuli (Bates et al. 2008; Gillam et al. 2007). Lab experiments with Kuhl's pipistrelle (*Pipistrellus kuhlii*) found that stimuli mimicking interference from many conspecifics induced more intense and longer pulse emissions that were accompanied by spectral shifts, but the changes in pulse frequency were uncorrelated with extent of overlap between the bat's own pulses and the playback stimuli (Amichai et al. 2015). This favors an interpretation that the spectral shifts are an unintended consequence of the Lombard effect. A prominent Lombard effect as well as an increase in pulse emission rate was also recorded from pale spear-nosed bats (*Phyllostomus discolor*) (Luo et al. 2015b), yet another mechanism for improving signal detectability that is presumably available to all bats.

It seems then that bats have multiple options for improving the detection of their echoes under noisy conditions. Increasing call intensity and repetition rate is a universal mammalian strategy for improving signal detection in noise (Brumm and Slabbekoorn 2005), and clearly echolocating bats take advantage of these fundamental strategies. Additionally, some bats display the capacity to selectively manipulate the spectral parameters of their pulse emissions, depending on the behavioral context and nature of the interfering noise. Solitary foraging bats are unlikely to encounter conspecific sources of sustained acoustic interference that demand anything more than a quick change in trajectory, but bats are social animals and when they swarm, forage or roost in groups a more comprehensive strategy for echolocating in noisy conditions may benefit them.

4.7 Conclusions and Future Work

Field studies and lab experiments confirm that even though bats are remarkably capable of hearing and echolocating under noisy conditions, bat sonar systems are still sensitive to environmental noise, including the sounds of other bats. Background noise has influenced the evolution of echolocation through auditory physiology, vocal manipulations, and shaping the behavioral limits of biosonar performance. There are still many questions about the extent to which bats are challenged by noise in their natural environments, and especially how they might be negatively impacted by anthropogenic noise pollution. Some animals like songbirds have managed to flourish in urban environments, but there is also evidence that urban noise has recently shaped birdsong acoustic properties. Should similar effects be anticipated in bats that are otherwise able to survive in and around human habitats? The prevalence and efficacy of jamming avoidance behaviors are still in doubt; additional studies in a broader range of species under natural conditions are needed to clarify whether or not bats are truly attempting to enhance the recognition of their own echoes or instead using some other adaptive strategy to find their signals through the noise. Noise stimuli continue to be a useful tool for exploring the psychophysics and physiology of the bat's sonar processing circuitry. The experiments outlined above have revealed some interesting clues, but many questions remain about how a pulse and an echo are encoded, stored and manipulated in the bat's brain.

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Part III
Ecology

Shahroukh Mistry

At the first NASBR symposium in 1970, presentations examining the ecology of bats dominated the meeting with almost half of all presentations. This pattern has persisted throughout the last half-century and continues to this day, with emphasis on many topics, including habitat use, diet, temperature, social interactions and migration patterns. This section exemplifies the continuity of ecology as a major theme throughout the history of NABSR with three chapters that all continue the theme of presentations at the original meeting in Tucson.

Roy Horst was instrumental in organizing the first, and many subsequent, meetings of NASBR. At the 1970 symposium, Horst and Youngkin presented a paper entitled *Respiratory Water Loss in the Vampire Bat Desmodus rotundus* where they describe the water recovery ability of vampire bats during exhalation as an adaptation to arid environments, similar to that seen in kangaroo rats. Arid environments, and adaptations by bats, appear to be important for bat diversity and population viability, as Adams and Hayes describe in their chapter *The Importance of Water Availability to Bats: Climate Warming and Increasing Global Aridity*. Effects of climate change are likely to enhance xerification, and how well bats adapt to these changes will be crucial for their persistence. Water limitation has a critical impact on reproduction and the authors document declines in population size, richness and range, and describe models that help predict challenges bats will face in the future.

Philip Leitner and Albert Beck talked about population size variation in *Tadarida brasiliensis* in northern and central California at NASBR in 1970. This was a unique study of an uncommon scale. They already had seven years of longitudinal research at the time of presentation and had banded over 75,000 bats of which they recovered more than 10,000. Law and Blakey's chapter surveys our current knowledge about bats in temperate forests and what we know about their population dynamics. They

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identify specific hurdles to measuring and monitoring population and point to the need of long-term studies that allow for detection of changes in population size. Unlike mark-recapture studies similar to Leitner and Beck, modern studies increasingly use acoustic monitoring that can at best provide relative population estimates but cannot provide vital information needed for demographic analysis such as sex ratios, age structure, reproductive status, home range, migration, etc. Law and Blakey also emphasize the gap in our knowledge about forest fires and their impact on bat populations and stress that this should be a priority in the coming decades.

In 1970, Jim Findley presented a paper entitled *Phenetic Relationships in the Genus Myotis* that would set the stage for his seminal work on bat community structure and the role of multivariate analysis in clustering species based on morphology into feeding and foraging modes. Arita and Villalobos retrace the history of Findley's work and the role it has played in our understanding of communities, niche partitioning and the interplay between morphology, biogeography, and phylogeny. This approach is vital to our understanding of how bat communities will respond to perturbations from habitat loss, climate change and other factors that impact bats today and in the foreseeable future.

Chapter 5
All the Better to Eat You with: The Legacy of James S. Findley's Phenetic Approach to Bat Biology

Héctor T. Arita and Fabricio Villalobos

Abstract James S. Findley's 1970 presentation in the first NASBR advanced the idea of applying multivariate methods in the analysis of morphological and ecological traits of bats in the genus *Myotis*. With this "phenetic approach", Findley explored new research frontiers in a diverse array of disciplines, including numerical taxonomy (phenetics), historical biogeography, phylogenetic reconstruction, functional ecology, and niche theory. Findley recognized three ecomorphs within the genus, each associated with a distinct foraging strategy and proposed an assembly rule for ecological communities. He assigned taxonomic names to the ecomorphs, thus establishing a three-subgenus classification that was the standard arrangement until the end of the twentieth century. Some of Findley's innovative ideas have been abandoned or improved with modern analytical methods, but many of his findings are still current and the subject of active research.

Keywords Bat community ecology · Ecomorphology · *Leuconoe* · *Myotis* · Niche theory · *Selysius*

On November 28, 1970, the closing day of the Symposium on Bat Research in the Southwest (what came to be known as the first meeting of the North American Society for Bat Research or NASBR), James S. Findley presented an analysis of the "phenetic relationships in the genus *Myotis*". In just 68 words, the abstract of the paper advanced novel concepts on the link between morphological traits and feeding strategies among bat species:

> Centroid factor analysis reveals that the species of *Myotis* occur phrenetically [*sic*] in three major clusters, suggestive of three major modes of feeding and foraging. These are (1) water

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> surface foragers, (2) hovering surface gleaners, (3) aerial insect capturers. Each group is distinguished by a suite of morphological traits which seems to equip it for the postulated mode of life. Limited behavioral data seems to support the morphological hypothesis.

In the ensuing paper about his investigation, Findley (1972) associated each of the major phenetic clusters with an existing taxonomic name, thus classifying *Myotis* bats into three subgenera: *Leuconoe* (water surface foragers), *Myotis* (hovering surface gleaners), and *Selysius* (aerial insect capturers). He envisioned the three phenetic groups as monophyletic lines, which, considering the continental distribution of species, suggested a paleotropical origin for the genus. Findley went as far as considering the Malagasy mouse-eared bat (*Myotis goudoti*) "the most primitive" species of the genus, because of its set of conservative morphological traits.

Two subsequent publications extended the phenetic approach to the analysis of the morphological structure of bat communities. In the first, Findley (1973) proposed the then novel idea of using phenetic packing, measured as the distance between pairs of species in multivariate morphological space, as a metric of ecological diversity. In the second paper (Findley 1976), he went further and postulated the innovative hypothesis that bat phenetic assemblages in different parts of the world are formed by combinations of several similar, closely packed species and a few more distinct, isolated forms.

Fifty years ago, the first NASBR heralded a new era for chiropteran biology in North America. In the following years, up to the end of the twentieth century and beyond, bats would come to be model systems in testing revolutionary ideas in all major branches of biological research. Findley's presentation in the symposium signaled the start of a research program, "the phenetic approach", that was key in the development of this new era of bat biology, as it contributed to substantial advances in areas as varied as numerical taxonomy, multivariate morphometrics, phylogenetic reconstruction, historical biogeography, functional ecology, niche theory, and community ecology. In this chapter, we review the historical context in which Findley's ideas appeared, examine their role in the development of new lines of research at the end of the century, and evaluate their present-day status within current paradigms.

5.1 Findley's "Phenetic" Analysis of the Genus *Myotis*

In his 1970 presentation and in the resulting publications, Findley (1972, 1973) used the term "phenetic" in a rather broad sense, meaning the application of multivariate statistical analysis of measurements and morphological variables in exploring questions in systematics and ecology. Later in the 1970s, the name "phenetics" acquired a more restricted meaning, replacing the term "numerical taxonomy" to refer to the approach in which the classification of organisms is based on overall morphological similarity, measured with multivariate exploratory and clustering statistical methods. Soon after, a heated controversy ensued regarding the relative advantages of phenetic versus cladistic approaches (Hull 1988), In the end, the traditional clustering methods based on morphometrics were gradually replaced with the now widely accepted cladistic methods that group species in natural lineages based on shared derived characters.

Eventually, Findley's broader "phenetic approach" to the study of size and shape of organisms came to be known as "multivariate morphometrics", a technique with multiple applications in different areas of anatomical, ecological, and evolutionary research. Thus, Findley's (1972) seminal paper on the "phenetic relationships" of *Myotis* bats was far more than a taxonomic study, as it incorporated a series of complex, innovative ideas that encompassed areas beyond systematics, such as functional morphology, community ecology, and phylogenetics.

Findley (1972) collected morphological data for most of the nearly 60 *Myotis* species known then and grouped individuals in 114 operational taxonomic units (OTUs) to account for geographic variation in species with multiple samples. The 48 morphological variables included those associated with flight and echolocation features (wing and ear traits), with trophic apparatus (skull and dental measurements), and with different behavioral strategies for capturing prey (e.g. size and pilosity of the uropatagium, size of the tibia and of the hindfeet). Data were fed into the numerical taxonomy system (NT-SYS), a set of computational procedures developed by F. James Rohlf that at the time was the state of the art in multivariate statistical analysis. Factor analysis provided a three-dimensional exploratory depiction of the relative morphological distance among OTUs and of apparent groups. Minimum spanning trees and phenograms supported the initial results of the factor analysis, showing three major morphological clusters, each corresponding to a particular foraging strategy.

Findley assigned a subgeneric name to each cluster using those available from prior taxonomic work (Tate 1941): *Leuconoe* included species such as the Eurasian Daubenton's bat (*M. daubentonii*) and North America's little brown bat (*M. lucifugus*). These are relatively small and short-winged and have a combination of short legs and large, haired hindfeet. They also have wide skulls with long and broad toothrows. Findley found reports of bats in this group foraging around large bodies of water, and speculated that they use their enlarged hindfeet, rather than the wing membranes, to capture prey. Thus, he characterized these bats as the "water surface foragers".

Species in the subgenus *Myotis*, such as the North American fringed bat (*M. thysanodes*) and the European Natterer's bat (*M. nattereri*), tend to be larger, with long wings, ears, and legs, but small hindfeet. They have robust skulls with elongated toothrows. These "hovering surface gleaners" are slow flying, highly maneuverable bats that capture their prey directly from the substrate.

The subgenus *Selysius*, including forms such as the Palearctic whiskered bat (*M. mystacinus*) and the California myotis (*M. californicus*), is characterized by small bats with small feet, broad plagiopatagia, and short ears. Their skulls have short rostra with corresponding short toothrows. Bats in this group, the "aerial insect capturers", hunt airborne insects, capturing them using the uropatagium as a collecting net.

Findley (1972) considered his phenogram of the genus *Myotis* a reasonable reflection of the group's phylogeny, following the then prevailing paradigm (Colless 1970). He viewed each of the morphological clusters as real, independent lineages that had diversified in different parts of the world, thus accounting for the presence of representatives of the three groups on all continents.

Findley's "phenetic approach" included a series of assumptions or hypotheses that encompassed a wide gamut of areas of ecology and evolutionary biology. First, he advanced the idea that ecological and behavioral traits of species can be inferred by examining the morphology of individuals. Second, Findley's observation that the three groups are represented by different species in different continents points to a regular pattern in the niche structure of ecological communities. Third, using the numerical taxonomic approach to relate a phenogram to a phylogeny assumes macroevolutionary regularities that should result in a pattern in which more similar species are more closely related. Finally, the phylogenetic reconstruction of the continental distribution of taxa, and even the recognition of the "most primitive" form, implies a series of hypotheses of historical biogeography. In the following sections, we in turn examine each of these components of the phenetic approach.

5.2 Functional Morphology

Findley and Don Wilson, a former student, reviewed what was known at the end of the 1970s about the functional and ecological implications of chiropteran morphology (Findley and Wilson 1982). As they pointed out, the idea that size, shape, and other morphological features of animals reflect their ecological and behavioral traits goes back to Aristotle. It is the basis of what is now called functional morphology, ecological morphology, or "ecomorphology" in the broad sense (Dumont 2003; Swartz et al. 2003). In Findley's original study, morphological variables included those related to overall size (e.g. forearm length, head and body length) and those related to the two major features that define the foraging behavior of insectivorous bats: flight and echolocation (Arita and Fenton 1997). As in other contemporaneous studies (Fenton 1972), Findley incorporated measurements of the ear and tragus as proxy for hearing and echolocation traits, as well as several wing measurements to quantify flight features.

In a parallel study, Findley, Wilson, and Eugene Studier examined the ecological significance of wing morphology for a sample of 136 bat species representing 15 families (Findley et al. 1972). They used aspect ratio as a measure of wing shape. Aspect ratio is defined for any flying object as the ratio between some measure of length and some measure of width of the flying apparatus. In the case of bats, a practical approach is to measure wing length as the sum of the length of the forearm and the total length of the third digit, and to quantify width with the length of the fifth digit. Findley et al. (1972) found a close positive correlation between aspect ratio and flight speed, that is, they showed that bats with relatively long and narrow wings were faster than species with relatively short and wide wings. The latter were found to be forest dwellers, whereas the former tended to forage in open spaces. By the end of the twentieth century, these pioneering observations were confirmed and were the basis for detailed studies on the functional morphology of bat wings (Norberg 1994; Norberg and Rayner 1987), and the ecological implications of such patterns (Aldridge and Rautenbach 1987).

Findley (1972) included also a series of measurements of the skull and the trophic apparatus and related them to the feeding preferences of *Myotis* bats. In the NASBR conferences of 1973 and 1975, Patricia Freeman, then one of his students, presented papers corroborating a close correspondence between cranial and mandibular morphology and the type of food preferred by insectivorous bats, particularly in relation to size of the prey and its hardness (Freeman 1979, 1981). This approach to functional morphology has been largely applied to several groups of animalivorous bats and has been extended to frugivorous and nectar-feeding species as well (reviewed by Dumont 2003; Swartz et al. 2003).

Correspondence between morphology and feeding strategies among *Myotis* that Findley inferred has been confirmed by observational studies and reviews (Fenton and Bogdanowicz 2002; Ghazali et al. 2017; Segura-Trujillo et al. 2018). Findley's clusters or groups of species with similar morphologies (and inferred similar ecological niches) are conceptually equivalent to what Losos et al. (1998) called "ecomorphs". The same ecomorphs of the lizard genus *Anolis* are found on each of the islands of the Greater Antilles, in a pattern resembling *Myotis*: each of the ecomorphs (water surface foragers, subgenus *Leuconoe*; surface gleaners, subgenus *Myotis*; aerial feeders, subgenus *Selysius*) occurs on all continental masses.

Findley's predictions about behavioral and ecological strategies for each ecomorph based on fragmentary and mostly anecdotal data have proven to be surprisingly accurate. For example, Kalko and Schnitzler (1989) used stroboscopic photography and high-speed ultrasound recordings to document the foraging behavior of Daubenton's bats (*M. daubentonii*) eating small flies and mayflies that gather over bodies of water. They found that the search flights of this bat are generally within 30 cm of the surface of the water and that, after food is detected, the bat descends and uses its interfemoral membrane and feet to capture the prey. Almost immediately the prey is consumed, and the bat reassumes search flight mode. This behavioral pattern corresponds to Findley's description of the feeding strategy of his ecomorph of water surface foragers, or subgenus *Leuconoe*, of which *M. daubentonii* is the type species.

Similarly, observational data have mostly confirmed Findley's inferred foraging strategies of the other two ecomorphs. Species of the subgenus *Myotis* are surface gleaners that locate and capture prey on surfaces. Species of *Selysius* are aerial feeders that capture airborne prey with the aid of the uropatagium and wing membranes (Fenton and Bogdanowicz 2002; Ghazali et al. 2017). A recent compilation of data from 18 field studies reveals that, based on the proportions of different arthropod prey in the diet, bats of the genus *Myotis* cluster in three major groups that correspond to Findley's three ecomorphs (Segura-Trujillo et al. 2018).

In summary, the fundamental premise of Findley's phenetic approach, that ecological function and morphological structure are closely tied has been fully confirmed, both in a general way and regarding his inferences about the three major ecomorphs within the genus *Myotis*.

5.3 Ecomorphology and the Structure of Bat Communities

Findley (1973) advanced the idea of measuring the diversity of assemblages of species with a phenetic metric based on the average taxonomic distance between pairs of species in a morphological multivariate space. To test the idea, he used data from his 1972 paper to show that, independently of species richness, *Myotis* assemblages of the Old World were more diverse than their American counterparts, because the former consistently encompassed wider morphological spaces.

Extending the idea of using the phenetic composition of bat assemblages to analyze the structure of ecological communities, Findley (1976) developed a theoretical model in which chiropteran communities were typically formed by many closely packed species and a reduced number of more isolated taxa. He compared bat assemblages from different continents to confirm the generality of his rule. In the following years, Findley and some of his students conducted further research on the morphological structure of bat communities and found the same basic structure in species assemblages from sites as dissimilar as Zambia and several localities in tropical and temperate North America (Findley and Black 1983; Schum 1984).

Findley's ideas on the structure of bat communities (Findley 1993) were based on two dominating paradigms of the early 1970s: numerical taxonomy (phenetics) in systematics (Sneath and Sokal 1973) and niche theory in community ecology (Diamond 1975). Findley's (1973, 1976) proposal of using morphometric distances as measures of ecological similarity, ecological packing, and diversity were natural extensions of numerical taxonomy metrics to the quantification of niche overlap and character displacement. Findley's main contribution in this area was to extend the idea of measuring niche parameters in a multivariate morphological space. It was not until 1975 that this idea reached the mainstream literature on niche theory, when Karr and James published their chapter on "ecomorphological configurations" in the volume honoring Robert MacArthur (Karr and James 1975). From then on, Findley's phenetic approach to the analysis of ecological communities was called "ecomorphology" (in the restricted sense), unfortunately without acknowledging Findley's work.

By the late 1970s, the basic paradigms of niche theory came into question In particular, the fundamental idea that interspecific competition was the key force shaping the structure of ecological communities was subjected to extremely skeptical tests, constituting a major paradigm shift in the history of ecological theory (Chase and Leibold 2003). Findley's model of community structure, based on classical niche theory, did not pass the battery of new tests, such as the randomization analyses known as null models, which contrast observed patterns against statistical distributions generated by repeated assemblages of randomly generated communities.

Nevertheless, even if the details of Findley's model did not prove to be correct, his original idea of examining bat communities as collections of points in multivariate morphological space continued to be a useful tool. Willig and Moulton (1989), for example, examined the structure of Neotropical bat assemblages by assessing the relative contribution of stochastic and deterministic processes in shaping the multivariate morphological space. By testing hypotheses with different null models, they found that bat assemblages did not have more structure than what would be expected by random sampling of taxa from a continental pool. Similarly, Moreno et al. (2006) found non-significant differences in species packing in multivariate space for bat assemblages in Central Mexico with varying species richness. Finally, Villalobos and Arita (2014) found that local communities of bats were in general not significantly different in morphological space from random samples taken from regional assemblages.

To summarize, Findley's idea of using multivariate morphological space to describe patterns in the organization of ecological communities was an advanced concept when first proposed and is still a powerful tool. However, his particular model of bat community organization could not be confirmed by subsequent studies of species assemblages of bats and other vertebrates.

5.4 Systematics of *Myotis*

Findley's (1972) first paper on the phenetic relationships of *Myotis* species focused on the systematic implications of the relationship between morphology and foraging strategies. Following the standard procedures of numerical taxonomy, Findley created a phenogram by subjecting his database of 48 morphological variables and 114 OTUs to a cluster analysis. The result confirmed the clustering of *Myotis* species in three groups (the ecomorphs in the ecological context). Findley interpreted his phenogram as a reflection of a real phylogeny for the genus *Myotis*, and thus considered his three ecomorphs valid taxonomic units.

Findley selected three of the seven subgeneric names available from Tate's (1941) taxonomic review of Old World *Myotis*. The cluster including *M. mystacinus* (the aerial feeding bats) was assigned to the subgenus *Selysius* Bonaparte, 1841. The cluster containing *M. daubentonii* (the water surface foragers) was named *Leuconoe* Boie, 1830. The surface gleaners were assigned to the subgenus *Myotis* Kaup, 1829. This arrangement of the genus *Myotis* in three subgenera persisted until about 2000 as the standard classification of the group. Koopman (1994) recognized the three-subgenus arrangement and added a fourth subgenus, *Cistugo*, for two African species later assigned to a separate genus (Lack et al. 2010), which de facto returned the arrangement of the *Myotis* genus to a three-subgenus scheme.

By the end of the century, however, Findley's arrangement came under scrutiny. Godawa Stormark (1998) used dental features to generate a phenogram of Old World species of *Myotis*, and found that the three putative subgenera were not natural groups. Cladistic analyses based on molecular data provided the same picture (Ruedi and Mayer 2001; Lack et al. 2010), corroborating that the division of *Myotis* into subgeneric categories is unwarranted (Simmons 2005). Despite this, the names leuconoe, myotis, and selysius (with no italics) are still used to refer not to Findley's taxonomic groups but to his ecomorphs (Ghazali et al. 2017; Segura-Trujillo et al. 2018). We believe that the use of taxonomic names to refer to ecological morphotypes is misleading but admit that this practice reflects the continuing impact that Findley's work has had on various disciplines.

In the 50 years since Findley's pioneering research, the number of species in the genus *Myotis* has increased from 60 to well over 100 (103 in Simmons 2005, 137 in the Mammal Diversity Database 2019) and continues to grow with each new survey or reassessment of bat faunas. Quite fittingly, one of the additions to the list of species in the genus was *Myotis findleyi*, a taxon endemic to Tres Marias islands in Western Mexico, which was described by Michael Bogan, one of Findley's doctoral students (Bogan 1978).

It is now clear that the phenetic approach is of little help in dealing with taxonomic problems posed by such large and dynamic groups as the genus *Myotis* (Platt II et al. 2017). Curiously, new studies using molecular data have failed to find natural groups within the genus that could warrant a meaningful subgeneric classification, but some of them end up discussing Findley's arrangement in three morphological groups. Thus, Findley's original quest for patterns in the evolution and classification of the genus *Myotis* is still an active area of research.

5.5 The Origin and Evolution of *Myotis* Bats

Findley (1972) attempted the reconstruction of the evolutionary history of the genus *Myotis* based on the results of his phenetic analysis. In the context of the prevailing paradigms in the early 1970s, Findley's conclusions seemed quite reasonable, but modern reinterpretations of his data and analyses based on alternative paradigms provide a different narrative for the evolution of the genus.

Findley faced in 1972 an evolutionary conundrum analogous to what Losos et al. (1998) found when studying the assemblages of *Anolis* lizards in the Greater Antilles. Both *Myotis* bats and *Anolis* lizards could be grouped into sets of species defined by morphological features that could be directly related to ecological and behavioral attributes. In other words, both the lizards and the bats clustered in clear ecomorphs. Moreover, just as the six *Anolis* ecomorphs occur on each of the four islands of the Greater Antilles, the three *Myotis* ecomorphs are present on all continents in the world. Even recognizing the possibility that the global distributional pattern of *Myotis* ecomorphs could be explained by a process of evolutionary convergence, Findley was convinced that phenograms were adequate reflections of phylogenies and concluded that his three taxonomic groups were independent lineages. In Findley's interpretation, each ecomorph appeared once and subsequently dispersed and diversified in different continents. This interpretation, we know now, was wrong.

Losos and collaborators (1998) faced their conundrum from the vantage point of modern cladistic reconstructions of phylogenetic histories that are independent of the morphological data. Losos et al. could therefore test statistically the two major hypotheses explaining the distributional pattern of *Anolis* lizards: either each ecomorph had evolved once and had invaded the four islands or every ecomorph had evolved independently in each island, through a process of convergent evolution. The statistical contrasts of several competing models showed that the most likely scenario was that ecomorphs had indeed appeared independently in each of the islands.

Phylogenetic reconstructions of the evolutionary history of the genus *Myotis* based on molecular data unequivocally show that Findley's ecomorphs are not monophyletic groups (Ghazali et al. 2017; Ruedi et al. 2013; Morales et al. 2020). The whole New World assemblage of *Myotis* species, for example, forms a single clade that split from the Old World group approximately 19 million years ago, and the ancestor of this American clade was probably a water surface forager (Ghazali et al. 2017). This implies that the aerial feeders and the surface gleaners that presently occur in North America evolved there, independently of their morphological counterparts in the Old World.

Findley (1972) identified the Malagasy mouse-eared bat (*M. goudoti*) as the "most primitive" representative of the genus. He reasoned that the least derived OTU in his database should be the one with the shortest average distance to all other OTUs, that is, the taxon closest to the centroid of the three-dimensional morphospace. Findley, however, did not suggest that this bat, or another taxon with a similar array of morphological features, was the oldest representative of the genus. Modern phylogenetic reconstructions place *M. goudoti* well inside a relatively species-poor African clade that split from the Eurasian group 17 million years ago (Ruedi et al. 2013).

To look for the center of origin of the genus, Findley (1972) examined the continental distribution of taxa and identified the tropical eastern portion of Asia as the most diverse area, not only in number of species but in morphological diversity, measured with the length of the minimum spanning tree in morphological space (Findley 1973). In comparison, the North American *Myotis* assemblage has a lower morphological diversity, meaning that fewer divergent species occur there. Therefore, Findley pointed to tropical eastern Asia as the possible cradle of the radiation of *Myotis* bats. This speculation, based on limited evidence, turned out to be correct, as confirmed by cladistic analyses of molecular data (Ruedi et al. 2013).

More recently, Ruedi et al. (2015) found that the Formosan broad-muzzled bat (*M. latirostris*), a taxon endemic to Taiwan that in Findley's study appeared embedded within the *M. muricola* group of the *Selysius* subgenus, is the sister taxon to all other *Myotis* bats. Ruedi et al. (2015) have removed *latirostris* from *Myotis* and have assigned it, along with two newly described species also endemic to Taiwan, to the genus *Submyotodon*, a generic name available from the paleontological literature. This is an extreme example of morphological and ecological convergence between species belonging to different genera (*Submyotodon latirostris* and *Myotis muricola*) that have developed almost identical external morphologies (that of the ecomorph of aerial feeders) through independent evolutionary lines that diverged from each other more than 20 million years ago.

Since the sister taxon of the *Myotis* clade is a bat with the morphology of an aerial feeder, it is reasonable to assume that this ecomorph is the ancestral state for the genus. In fact, since Findley (1972), most studies have inferred that either the aerial-feeder or the water-surface-forager ecomorph is the ancestral form, whereas the gleaners are considered derived taxa (Morales et al. 2020). Ghazali et al. (2017) showed that the transitions between the aerial-feeder and the water-surface-forager ecomorphs are the most likely evolutionary paths, confirming their possible ancestral status. It is also likely that the ancestor of all New World species of *Myotis* belonged to the group of water surface foragers and that the other two ecomorphs evolved in North America independently of their Eurasian counterparts (Ghazali et al. 2017). This inferred pattern is supported by the fact that the Neotropical fauna of *Myotis* (which presumably derive directly from the Nearctic fauna) harbors species only of the water forager ecomorph.

Findley (1972) did not examine the evolutionary origins of the genus *Myotis*, because his phenetic method could not be applied to the scant fossil material available at the time. However, derived from studies that have examined some of Findley's hypotheses, and from the analysis of fossil material now available, we have a better idea of the origins and early evolution of the *Myotis* clade. The most extensive reconstruction of the phylogeny of *Myotis* (Ruedi et al. 2013, confirmed by Ghazali et al. 2017) provides a rather simple splitting pattern for major clades and a more complex sequence of diversification events for particular groups within those larger clades. Major events include: (1) the split of the traditional *Myotis* genus (including *latirostris*) from other vespertilionids, 26.2 MYA; (2) The split of *M. latirostris* (now *Submyotodon latirostris*) from all other *Myotis* taxa, some 20.9 MYA; (3) the split of the *Myotis* line into two major groups, the New World and the Old World clades, 18.7 MYA; (4) the separation of the African clade, a rather depauperate assemblage (Patterson et al. 2019), 17.0 MYA; and (5) the start of the diversification in the Nearctic clade, with the appearance of the ancestors of the Neotropical lineage, 12.3 MYA.

The estimates of 26 and 21 million years for the age of the *Myotis* clade, in the broad and the restricted sense, respectively, are consistent with the extensive fossil record of the genus in Europe, which spans the late Oligocene (23 MYA) to the Holocene. However, a fossil recently described from the early Oligocene (33.9 MYA) of Belgium, named *Myotis belgicus*, is 8 or 13 million years older than the putative common ancestor of *Myotis* bats (Gunnell et al. 2017). This finding will surely stimulate a new series of analyses to reconcile the evolutionary perspectives provided by the paleontological and the molecular approaches.

5.6 Epilogue

Findley's presentation of his "phenetic approach" in the first NASBR meeting was the beginning of a revolutionary line of research, with ramifications in a diverse set of disciplines. It was also the start of a tradition in bat research that inspired his numerous students and colleagues (Geluso and Wilson 1997), and a cadre of younger researchers that are still exploring the ecomorphology research paths first discovered by Findley's pioneering work. Two of Findley's students, Patricia Freeman and Don Wilson received the Gerrit S. Miller Jr. Award from NASBR as have Betsy Dumont and Sharon Swartz, who followed the tradition established by Findley and studied functional and ecological morphology of bats. Upon his retirement in 1997 and "in recognition of his long and distinguished career in bat research", Findley was awarded a life membership in NASBR. We have shown that some premises and predictions of the phenetic approach have been proven to be wrong in the light of modern analyses, but many others have been corroborated by recent research, or adapted to new paradigms. The visionary initiatives of Findley have contributed to novel lines of research that have been explored with innovative methods and that have inspired a considerable number of research projects. Fifty years after that November afternoon when he advanced his revolutionary ideas, the legacy of James S. Findley is alive in a new generation of bat biologists that share his curiosity and innovative spirit.

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Chapter 6
Bats in Temperate Forests: Where Are the Trends in Bat Populations?

Bradley S. Law and Rachel V. Blakey

Abstract Understanding bat population dynamics is crucial to evaluating the effects of forest disturbances, however this remains a significant knowledge gap in bat ecology. In this chapter, we review different approaches to long-term studies of bat populations in temperate forests including landscape-scale monitoring programs and localized mark-recapture studies of banded bats. We particularly focus on studies that assess long-term changes to populations in managed forests, given that these forests offer opportunities to experimentally test bat response to disturbances via forest management treatments. We reviewed available NASBR abstracts from 1970 to 2018 to highlight trends in North American bat population research. While use of acoustic detectors has increased the ease with which researchers can conduct landscape-scale studies, these methods are limited to generating relative population indices (e.g. activity, occupancy) as individual bats are not identified. However, as use of acoustic methods continues to grow, use of mark-recapture studies, which allow researchers to measure bat population size and demographic rates, has decreased. Furthermore, the majority of studies of bats in forests do not extend past 1 year. When investigating ongoing effects of disturbance on bats in forests, large-scale long-term studies using population indices are needed to track trends at large spatial scales, and to capture unpredictable events like fire, drought and flood. Landscape-scale studies can also incentivize more localized experimental mark-recapture studies, ideally in partnership with forest managers. We highlight several long-term studies at the landscape and localized scales that have helped us better understand bat population dynamics in managed forests. We also highlight fire (wildfire and prescribed) as another key forest disturbance that should be the subject of ongoing studies for bats. Long-term research is vital for understanding long-lived, dynamic systems like forests, yet for bats, such research is notably scarce.

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6.1 Foundation Studies of Bat Populations

Questions about population dynamics have interested members of the North American Society for Bat Research (NASBR) since the first meetings of the society. In the early years of NASBR, research on population ecology of bats was dominated by long-term mark-recapture studies. At the first NASBR meeting in 1970, Philip Leitner and Albert J. Beck presented the results of a 7-year study, where more than 75,000 Mexican free-tailed bats (*Tadarida brasiliensis*) were banded in the state of California, thereby revealing sex-based differences in seasonal movements and a lack of long-distance migratory behavior within the population. Long-term population-based research by Merlin Tuttle on gray bats (*Myotis grisescens*), beginning in the 1960s, contributed essential data about an endangered bat species leading to its protection and recovery efforts.

Around the same time, ultrasonic detectors were emerging as an effective way to monitor bat populations remotely, championed during talks in early meetings by NASBR members Brock Fenton in 1971 and Tom Kunz in 1972. While the use of acoustic detectors has increased, allowing for the emergence of national and international monitoring programs for entire bat communities, the study of bat populations using mark-recapture techniques has decreased. A key driver of the decrease in bat mark-recapture studies was a moratorium on bat banding by the US Fish and Wildlife Service and a resolution to end banding by the American Society of Mammalogists in 1973 due to observed harmful effects on banded bats. These trends are reflected in the relative proportions of abstracts presented at NASBR meetings concerning acoustic and mark-recapture over the last 50 years (Fig. 6.1).

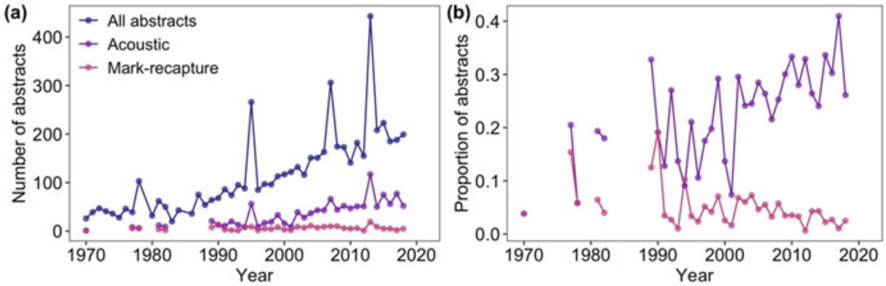

Fig. 6.1 The number (**a**) and proportion (**b**) of studies (abstracts) from NASBR conferences (1970–2018, both oral and poster presentations were included) that presented acoustic research vs. mark-recapture research. The total number of abstracts presented at the conference is shown in *blue*, peaks indicate years when NASBR was combined with the International Bat Research Conference (IBRC). Years are missing where only titles were available

Abstracts were searched manually for key words “call”, “acoustic”, “sonar”, “detector” (acoustic) and “recapture”, “band”, “mark” (mark-recapture). At the 2010 NASBR meeting in Denver, three NASBR scientists (Scott Reynolds, Eric Britzke, and Susan Loeb) called for a re-evaluation of the moratorium on banding, given the availability of improved bands and urgent threats to bat populations, though to date, no formal re-evaluation appears to have taken place. Past opposition to bands and adoption of improved bands has also occurred in Australia and Europe.

Shifts in research survey methodologies have implications for our understanding of bat populations. The use of ultrasonic detectors means we can collect data across wide geographic areas simultaneously for a greater range of species and at a fraction of the cost of trapping surveys. However, an important distinction between mark-recapture techniques and acoustic surveys is that the latter can only give information about relative activity levels (a population index) and not individual bats. Hence, while it can be argued that you can learn about population dynamics via measurement of population status, this is limited to geographic distribution of a population and meta-population dynamics. Fluctuations in abundance and demographic rates of bat populations can only be measured by methods that allow identification of individuals. In this chapter, we discuss the importance of studying populations using both techniques because acoustic studies are well suited to landscape-scale population indices and mark-recapture studies reveal population dynamics at local and sometimes landscape scales.

6.2 The Importance of Understanding Bat Population Dynamics in Forests

Most studies of bat population dynamics have focused on colonial bats roosting in subterranean or artificial structures (e.g. Sendor and Simon 2003; Frick et al. 2010), whereas little research has been done on forest bats using natural roosts in tree hollows, where only a small proportion of the population may be detected at roosts or in traps (Pryde et al. 2005; O’Shea et al. 2010). Forests are one of the most important habitats for bats, offering resources for both roosting and foraging. Humans are also heavily reliant on forest resources, particularly timber. Consequently, forests are highly managed and modified in many areas. Indeed, logging and harvesting of plants has been listed as the biggest global risk to bats, although that categorization didn’t distinguish between deforestation, and timber harvesting with or without different environmental standards (Frick et al. 2019). While deforestation clearly results in habitat loss, understanding the effects of silvicultural management and regeneration of forests and its associated disturbances remains of great importance to the conservation of bats (Law et al. 2016). There is a large body of work that has investigated many different components of the ecology of bats in forests and this has challenged our understanding of how bats interact with the complexity of forests and human-imposed disturbances (Lacki et al. 2007).

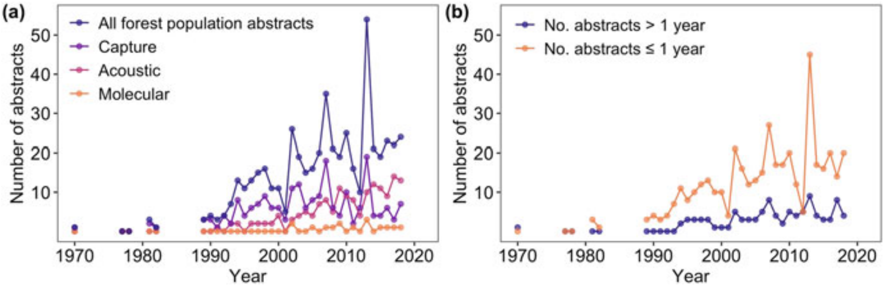

Fig. 6.2 NASBR abstracts (1970–2018) that investigated bat ecology in forests: (**a**) Acoustic (all studies that used acoustics to investigate bat populations); capture (all studies where bats were physically captured to investigate bat populations); and molecular (studies using molecular techniques to investigate bat populations). Other methods were included in the "All Forest Population abstracts", but are not shown separately. (**b**) Numbers of studies with a duration longer than 1 year/season, compared to studies with a duration less than or equal to 1 year or unspecified. Years are missing where only titles were available

However, understanding population dynamics of bats in forests remains a significant knowledge gap, especially in relation to forest disturbances such as timber harvesting and fire (Weller 2007; Law et al. 2016).

One of the earliest ultrasonic studies of bats in forests of northwestern United States found that activity (i.e. number of passes) was 3–10 times greater in old growth forest (>165 years) than in younger forest (Thomas 1988). Subsequent advances in radio-telemetry as well as ultrasonic equipment and analysis have vastly improved our knowledge of how various species use forests under different kinds of management. By the mid-1990s research was sufficiently advanced to allow for a North American symposium exclusively on bats and forests (Barclay and Brigham 1995), followed soon after by a review of the use of Australian forests by bats (Law 1996). None of the papers in these collections tackled the issue of trends in bat populations in relation to forestry practices, but both stimulated an explosion of studies on bats in a forest context. This can be seen in the continued increase in the number of abstracts investigating bat ecology in forests from NASBR meetings in the 1990s onwards (Fig. 6.2a). Abstracts were searched manually for the key word "forest" and limited to empirical studies with a response variable broadly consistent with population research (e.g. abundance, activity, presence, use). These abstracts were further manually separated into those that investigated effects of forest management practices on bats and those that investigated effects of fire (Fig. 6.3). Weller (2007) reviewed the many challenges of monitoring bats (see also O'Shea et al. 2004) and considered the viability of bat populations in forests, but only a single example evaluating a change in site occupancy between 2 years was discussed (Weller et al. 2002). A plea for large-scale long-term experimental investigations for evaluating the effects of management practices on forest bats also appeared at this time (Brigham 2007). The most recent review of bats and forestry made the same now familiar conclusion (Law et al. 2016). Indeed, the majority of studies presented at NASBR (1970–2018) dealing with bat ecology in forests extended for a single

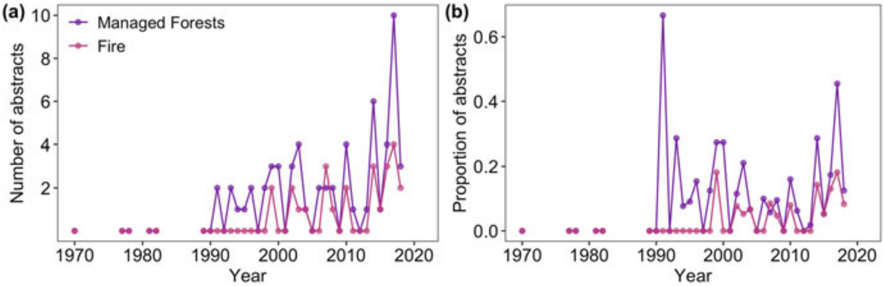

Fig. 6.3 The number (**a**) and proportion (**b**) of studies on bat populations in forests from NASBR conferences (1970–2018) that investigated forestry or forest management practices (*purple*) and either prescribed or wildfire (*pink*). Prescribed fire studies were counted in both forestry and fire categories. Abstracts were identified manually from the subset of bat population studies in forests identified in Fig. 6.2. Note the apparent spike in abstracts on forest management practices in 1991 constitutes only two papers (from a total of three papers regarding bat populations in forests)

year or season (Fig. 6.2b). Data on landscape-scale population estimates of bats are few and it is unclear to what extent the increasing loss of the unharvested forest matrix will lead to declines in populations of forest bats (Law et al. 2016), though this issue is receiving increasing research attention (Fig. 6.3). Population studies are likely to provide the ultimate test of the effectiveness of a silvicultural regime, especially when such studies take a long-term perspective, and this is the impetus behind our review.

6.3 Landscape-Scale Monitoring of Population Indices

Monitoring is often proposed as central to threatened species management and is frequently listed in recovery action plans (Lindenmayer and Franklin 2002). Such an approach is needed to increase our confidence about the effectiveness of wildlife protection measures. A monitoring design based on sound science with a high level of precision must be the goal. Clearly, it is sensible to be forewarned of any potential changes in the status of common species, as well as those currently listed as threatened. The scale over which many vertebrates move complicates the interpretation of trends through time, especially in relation to disturbance events. Given that bats fly and feed to varying extents across the landscape, a landscape scale is needed for effective monitoring of bats. Due to logistical difficulties, typically population indices are the target for large-scale monitoring programs and for bats these could focus on either changes in activity levels or occupancy (Frick 2013). Optimizing ultrasonic sampling effort for bats has led to recommendations that bat activity levels are more sensitive for detecting change than site occupancy, except for rarer species (Law et al. 2015).

Long-term monitoring programs have been initiated in North America (Loeb et al. 2015) and the United Kingdom (Barlow et al. 2015), with the explicit aim of detecting relative changes in population indices at the national scale. Regional-scale bat monitoring programs have been initiated globally, for example in New Zealand (O'Donnell 2002) and Australia (Law et al. 2015). One such regional study is called the 'Bat Grid', an interagency bat monitoring program in Oregon and Washington, USA (~430,000 km^2; Rodhouse et al. 2015). Model-based spatially explicit predictions of bat distributions from capture and acoustic surveys were made for 14 species using an 8-year monitoring dataset. Annual turnover in occurrence was generally low for these species, and occurrence probabilities were mostly stable. Although the spatial scale did not specifically address forestry issues, all seven species that were modeled in relation to snag abundance showed at least a modest positive association (Rodhouse et al. 2015). Such programs have the potential for being updated over time and for zooming in on forestry landscapes using more intensive sampling to capture broad changes in population indices in those landscapes.

Hibernation counts are an alternative to acoustic indices for assessing temporal change. Counts in the eastern United States undertaken between 1999 and 2011, were used to analyze long-term regional population trajectories (Ingersoll et al. 2013). Declining populations were found among a number of species, with declines evident prior to the spread of white-nose syndrome (2008–2010). Declines were suggested to result from multiple threats, but the influence of forest management practices was not highlighted.

6.4 Local Studies of Population Dynamics

Landscape-scale monitoring programs often measure population indices like occupancy and activity, rather than the dynamics of bat populations, such as estimates of mortality or survival, in relation to different silvicultural practices. Such data require intensive trapping and marking of local populations at local sites, though given the movement made by bats, study areas would still be expected to extend over a few 100 ha at minimum. Studies on the mark-recapture of bats have a relatively long history and featured prominently in presentations at early NASBR meetings. More recently, new analytical methods have provided more robust approaches to dealing with assumptions required for these studies. Early reviews grappled with and recommended approaches needed to analyze such data for bats, including the special case of bats that roost in tree hollows (O'Shea et al. 2004). Most studies of bat population dynamics have focused on colonial bats roosting in subterranean or artificial structures (Frick et al. 2007, 2010; Papadatou et al. 2011) and their survival is sensitive to introduced predators (Pryde et al. 2005) and climate, including hot dry summers (Frick et al. 2010), warm winters (Pryde et al. 2005; Schorcht et al. 2009), and excessive rainfall (Hoyle et al. 2001). The emergence of white-nose syndrome in North America has also been a stimulus for gathering better data for bat population trends in relation to the spread of the fungus (Frick et al. 2010). Catastrophic events such as a severely cold winter have been highlighted as drivers of mortality in the European Bechstein's bat (*Myotis bechsteinii*) (Fleischer et al. 2017). Yet few studies exist for forest bats using natural roosts in tree hollows, where only a small proportion of the population may be detected (Pryde et al. 2005; O'Shea et al. 2010; O'Donnell et al. 2017).

The only study that we are aware of that has assessed population dynamics in relation to forestry practices was conducted within an experimental forest, located in a climate refuge, in Australia (Law et al. 2018a). Banding data for four species of vespertilionids were collected over 14 consecutive years. While the authors accounted for transient bats, they found that a large portion of the population remained resident, with a maximum time to recapture for an individual being 9 years. The effect of logging history (unlogged vs. 16–30 years post-logging regrowth) on apparent survival was minor and species-specific, with no detectable effect for two species, a positive effect for one and negative for the other. There was no effect of logging history on abundance or body condition for any species. Another recent long-term study compared population dynamics of a specialist trawling bat between two sites over 14 years where one site was impacted by forest harvest and some agricultural production, while the other was relatively undisturbed forest (Law et al. 2020). Similarly, this study found no difference in survival between the two sites, providing evidence that timber harvest with protective measures in place did not negatively influence the survival of this species (Law et al. 2020). One potential explanation for the negligible effect of forest harvesting on populations was the extent of landscape protection afforded to unlogged forest in the study area (i.e. retention forestry). Edges formed by internal forest tracks together with environmental protection measures mitigated the effects of dense regrowth and bats likely used these features at a local landscape scale. Additionally, retention forestry with riparian buffers protected foraging habitat for specialist trawlers like large-footed myotis. Such multi-scale forest management is recognized as a key component of achieving ecologically sustainable management in timber production forests (Lindenmayer and Franklin 2002; Law et al. 2016).

6.5 Frontiers for Temporal Studies of Bat Populations in Forests

Many of the biggest issues affecting bats in forests today were absent from early NASBR meetings. While the basic physics behind climate change has been understood for more than a century, ecologists have relatively recently revealed global effects of climate change on biodiversity with predicted worst case scenarios leading to a sixth global mass extinction (Bellard et al. 2012). Climate change is likely to have already affected bats in forests globally via range shifts (Lundy et al. 2010; Bullen and McKenzie 2011; Perry 2018) and disruption of migratory behaviors

(Adams 2018; Stepanian and Wainwright 2018). Furthermore, a suite of additional effects are anticipated, including greater range shifts and contractions (Rebelo et al. 2010; Aguiar et al. 2016) as well as disruptions to food webs (Pryde et al. 2005; Krauel et al. 2015). However, these predictions are rarely tested because they require long-term studies. Such studies in forests of the Western United States allowed Hayes and Adams (2017) to predict declines in populations of the fringed myotis (*Myotis thysanodes*) in a future with climate change. They pointed out that long-term mark-recapture data elucidating species-specific survival and fertility rates across environmental gradients would significantly improve future predictions. Looking to the future, only long-term studies, including those that identify individuals and those monitoring population generated indices, will reveal whether predicted climate refugia will buffer effects of changing or extreme climate events on bats (Law 2018; Law et al. 2018a).

Another consequence of climate change is an increase in catastrophic fires, as well as fire suppression. The increase in the incidence and severity of wildfire, and its effects on bats is receiving increasing attention from bat scientists and forest managers (Law et al. 2018b; Blakey et al. 2019; Fig. 6.3). Fire influences bat communities through direct disturbance, injury and mortality during the fire event, as well as structural changes in foraging habitat, creation and destruction of roosts and fluxes in prey populations. Studies of bats and wildfire are few and rarely included a temporal component given the unpredictable nature of wildfires. A south-eastern Australian study is the first to investigate the response of bat activity to severe wildfire including both pre-fire and unburned controls, with post-fire visits at 1 and 4 years after fire (Law et al. 2018b). This study found the effect of fire on species-level bat activity ranged from neutral to positive over this period, however, the effects of fire on bat roosts were not studied.

Prescribed fire is gaining traction as a forest management technique for both reducing risk of high severity fires, restoring historical forest structure and stimulating reproductive cycles of fire-dependent biota. While prescribed fire has received more research attention than wildfire, temporal studies are also scarce, with few surveying before and after fire (but see: Lacki et al. 2009; Inkster-Draper et al. 2013; Ford et al. 2016) and only one study assessing the response to repeated burning over a longer time period (Law et al. 2019). Importantly, no studies of bat response to fire have investigated bat abundance with respect to fire, with the vast majority of literature based on relative trends employing acoustic data. However, in a recent study in the Mediterranean region, lower proportions of reproductive individuals coincided with the year after a severe fire in *Hypsugo savii*.

Finally, population studies, both within hibernacula and during summer foraging, have been critical for tracking the effects of white-nose syndrome (WNS) on eastern North American bat populations (Reynolds et al. 2010; Pettit and O'Keefe 2017). As WNS spreads west where winter roost habitats are poorly known, understanding population dynamics will be critical to monitoring the spread and effects of this disease.

Alternatives to banding, such as passive-integrated-transponder (PIT) tags have revealed energetic trade-offs for hibernating bats (Willis 2017), social structure within maternity roosts (Garroway and Broders 2007) and survival rates of bats after pest control (O'Donnell et al. 2011; Edmonds et al. 2017), but their real advantage for population studies will be realized when electronic readers are more routinely employed in forests. Bats using natural roosts in hollow trees could be monitored less intrusively and this has the potential to yield vast amounts of data on social relations as well as traditional mark-recaptures for population studies. One recent application used a long-term data set based on PIT tags to monitor the longevity of use of an area by bats roosting in hollow trees (Bondo et al. 2019). Molecular techniques are increasingly being used to study bat populations in forests (Fig. 6.2a) and continue to advance our understanding of bat populations. For example, genetic mark-recapture studies show promise in estimation of population size and survival rates of cave-roosting species (Oyler-McCance et al. 2018).

6.6 Conclusion

Population trends are unknown for 57% of all bat species (Frick et al. 2019). Long-term research is vital for understanding long-lived, dynamic systems like forests, yet for bats such research is notable for its scarcity. Pressure on early career scientists to publish, the relatively short duration of graduate degrees, coupled with decreasing government spending on science, mean we are seeing increasingly ambitious scientific questions asked at very short temporal scales. For example, patterns found at seasonal or annual scales may not be representative of multi-year long-term patterns due to temporal changes in climate and evolution of forestry practices over time.

For forest bats, the unpredictable or logistically difficult nature of collecting pre-impact data for key disturbances like logging, prescribed burning and wildfire, mean the majority of studies that examine these disturbances use space-for-time rather than temporal designs. The view that bats are too difficult to include in long-term monitoring programs has been dispelled (Law 2018). Both landscape trend-monitoring of population indices (activity and occupancy) and more localized, intensive population studies are viable options that need prioritization for funding (Meyer 2015). National and regional landscape-scale monitoring programs of population indices should be continued and expanded, such programs will be needed to track bat response to long-term disturbances such as climate change, WNS and anthropogenic disturbances as well as unpredictable events like fire, drought and flood. Trends identified in landscape-scale monitoring programs can then trigger or be overlayed with long-term experimental research that tests specific disturbances on bat population dynamics at finer scales. This will require strengthening partnerships between bat researchers and forest managers and the implementation of adaptive management programs, where adaptive management approaches are followed with rigorous monitoring. NASBR is well positioned to highlight the need for such studies and where possible to support the inclusion of bats into broader biodiversity monitoring programs.

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Chapter 7
The Importance of Water Availability to Bats: Climate Warming and Increasing Global Aridity

Rick A. Adams and Mark A. Hayes

Abstract Environmental change due to climate warming is accelerating in most of the world's arid regions, pushing already xeric ecosystems towards drier conditions and expanding desert landscapes. These changes will alter community structures and species interactions globally. Because many arid regions, especially semi-arid zones, are relatively high in bat species richness, reactions of bat populations to increasing and intensifying droughts will affect food web dynamics and ecosystem services on nearly every continent. Although there is evidence that some species have pre-adaptations for surviving decreasing available water resources in arid regions, many species may succumb to the pace of climate warming and landscape xerification. As drought and aridity increase, many drinking sources will inevitably be lost, increasing competition for progressively limited resources, thereby affecting bats during the reproductive season when they are most vulnerable. Herein, we review how climate warming and increasing drought are currently altering bat population dynamics and model future viability of some species and populations. Documented declines in some bat populations, reductions in species richness, and changes in distributional ranges are already occurring in hardest hit areas and some models have been developed to predict future outcomes for bats living on the leading edge of climate disruption.

Keywords Bats · Climate change · Arid lands · Xerification · Water

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7.1 General Introduction

Globally, climate warming, changing precipitation patterns and disruptions in local stream hydrology have begun to alter bat populations and species distributions. In order to predict and potentially mitigate some effects of climate warming, data on bat ecophysiology, roost site ecology, distributional ranges, diet, water needs, and reproduction patterns for many taxonomic groups is necessary. The first symposium on North American bat research held in Tucson, AZ is replete with abstracts on these topics by early pioneers of bat ecophysiology, population ecology, and biogeography. The list includes Thomas Kunz, Terry Vaughan, Eugene Studier, Eldon Braun, Roy Horst, Roger Carpenter, James Findley, and Michael O'Farrell among others. Many of these conference abstracts led to peer-reviewed publications cited herein that are critically important to understanding bat physiology and behavior in relation to how climate warming is affecting bat populations 50 years later.

We integrate the results of these founding NASBR researchers with contemporary literature to understand and predict how bat populations and assemblages are changing, and will change in the future, due to increasing xerification of already arid regions. This question is of global concern and we review the literature to date as well as review our work based on 20 years of data collection in the semi-arid foothills of Boulder County, Colorado, USA. We also discuss the propensity of some bat species to persist in arid environments and describe how some may be predisposed to surviving the pace of climate change.

7.2 Global Arid Lands and Climate Change

Broadly speaking, arid lands are regions where evaporation exceeds precipitation. These areas comprise nearly 50% of global terrestrial habitats. Degrees of aridity vary and can be placed into four categories as measured by mean annual precipitation divided by mean annual evapotransporation (P/PET): Hyperarid Zones (0.03–0.05 P/PET) cover about 7.5% of Earth's land surface, Arid Zones (0.05–0.2 P/PET) account for about 12.1% land surface, Semiarid Zones (0.2–0.5 P/PET) occur on all continents and contribute 17.7%, and Dry Subhumid Zones (0.5–0.65 P/PET) cover about 9.9% of Earth's land surface (Barakat 2009; Fig. 7.1a).

Although the highest bat species richness and abundance follows the distribution of tropical rainforest, diversity is also remarkably high in many arid regions. For example, more than half the bat species known from Mongolia occur in arid and semiarid zones (Nyambayar et al. 2010) which compose most of Mongolia's landscapes. Similarly in the Kalahari Desert of South Africa, a landscape of sand dunes that receives <2.22 cm of rain annually supporting merely sparse ground vegetation and occasional acacia trees, sonar calls of 12 bat species from four families were detected at a few available water sources during the harsh dry season (Adams and

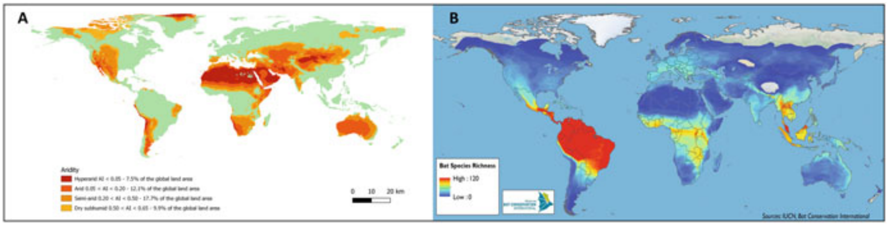

Fig. 7.1 (**a**) Distribution of the four types of arid lands recognized (Open Access, The Food and Agriculture Organization of the United Nations (FAO)). (**b**) Distribution of global bat species richness (Bat Conservation International Strategic Plan 2020–2025)

Kwiecinski 2018). By comparison, a similar number (19 species) was recorded in Kruger National Park, South Africa that receives only 15 mm of rain during the dry season (Adams and Kwiecinski unpublished data). High bat species diversity also occurs in arid environments of other countries (Mares 1992; Russo and Jones 2003; Korine and Pinshow 2004; Ojeda and Tabeni 2009; Rebelo et al. 2010; Korine et al. 2016; Sandoval and Barquez 2013).

One generalized trend of global climate change is a steady transition of all stages of arididity towards greater aridness (Huang et al. 2016) and these changes are being accelerated by positive feedback loops between soil and atmosphere (Zhou et al. 2019). So, the question becomes how bats currently living in these regions will react to increasing aridity and expanding drought-prone landscapes?

7.3 How Water Availability Relates to Bats in Arid Environments

Most bat species require access to reliable water sources for replenishing daily evaporative water losses and for many species water-emergent insects are important dietarily (Vaughan et al. 1996; Grindal et al. 1999; Ciechanowski 2002; Campbell 2009). Therefore, one would predict that increasing aridity would result in decreasing bat abundance and species richness at local and regional scales as water sources disappear. Globally, bats in arid regions concentrate activity over open water, even using urban swimming pools (Rydell et al. 1994; Walsh et al. 1995; Szewczak et al. 1998; Young and Ford 2000; Mickeviciene and Mickevicius 2001; Adams and Simmons 2002; Ciechanowski 2002; Russo and Jones 2003; Korine and Pinshow 2004; Williams and Dickman 2004; Anderson et al. 2006; Davie et al. 2012; Monamy et al. 2013; Korine et al. 2016) and this behavior is consistent even over elevational gradients in mountainous arid regions (McCain 2007). In many instances water availability may be seasonally or annually ephemeral and vary greatly in accessibility for bats of different body sizes and wing morphologies. Less agile species may be excluded from sites too small and cluttered with vegetation (Rabe and Rosenstock 2005; Racey 1998; Adams and Hayes 2008; Geluso and Geluso 2012).

This especially affects larger-bodied bats that may struggle to maintain the lower flight speeds necessary to drink from smaller, or vegetatively cluttered, water sources (Findley 1993).

Because water sources in arid environments commonly concentrate high-levels of bat activity in space and time (see Korine et al. 2016 for review), they may act as focal sources of complex interactions among species that are commonly segregated while foraging. Interactions among species vying for access at smaller water sources may influence the organization of bat assemblages at larger scales. For example, we found evidence for competative avoidance at crowded water holes in the semi-arid environments of Colorado. For example, we observed significant species-specific temporal partitioning of peak activity times by myotis species ranging in mass from 4 to 10 g in (Adams and Thibault 2006). In addition, the order of species arrivals varied in relation to the number of myotis species using the site. Curiously, species with greatest overlapping arrival times showed the greatest disparity in the number of individuals vying for drinking access, another indicator of competition. However, as a general pattern, it was the smaller-bodied myotis (*M. ciliolabrum and M. lucifugus*) that arrived earliest regardless of species richness at the site, indicating that body-size related evaporative water losses may be the dominant influencer of species arrival order, with competition a secondary effect that governed the number of individuals of each species that could access the site in a timely fashion.

Other studies have corroborated these patterns. For example, Commissaris (1961) recorded the visitation times of bats visiting two water holes in Arizona and subsequent analysis of his data also showed temporal displacement among species (Cockrum and Cross 1964). O’Farrell and Bradley (1970) found that greatest segregation in arrival times between the similarly-sized species *Pipistrellus hesperus* (now *Parastrellus hesperus*) and *Myotis californicus* at a desert spring in Nevada when water demands were highest. Possible competition potentially led to consistent temporal partitioning between similarly sized *Parastrellus hesperus* and *Myotis californicus* at 35 water sources in the Mojave Desert (Utah, USA) and this occurred independently of water source surface area (Lambert et al. 2018). In addition, artificial reductions in surface area of two sites by these authors resulted in higher overall activity, temporal partitioning, and measurable negative effects on drinking rates for both species. This further supports the hypothesis that competitive interactions for water in limiting environments would influence population numbers among coexisting species at local and possibly regional scales. This hypothesis is in need of further investigation and should be prioritized in light of increasing desertification globally.

7.4 Proximity of Water to Maternity Roosts

Data from various studies indicate that the location where water occurs on the landscape matters for bats. Water availability near nursery colonies may be critical for bats in arid environments as evidenced by a distinctive pattern of roost site clustering near reliable water sources when possible (McLean and Speakman 1999; Adams and Thibault 2006; Campbell 2009). Although the physiological and

Fig. 7.2 Infrared image of bat skimming a water source with PIT-tag plate antennae placed just below the water's surface. This system was used to quantify bat drinking activity of nonreproductive and lactating female *M. thysanodes*

reproductive cost to bats of water sources located close to maternity roosts is difficult to test, Tuttle (1976) found that lactating female gray bats (*Myotis grisescens*) traveling longer distances to find food and water experienced significantly longer gestation times indicating slower offspring development. Physiological effects of restricted water availability on adults and juveniles may also be quite severe. In laboratory and field tests, individuals lost as much as 31% of their body mass during 12-h roosting bouts under conditions of moderate high temperatures (27.8 °C) with relative humidities of 20% (Studier 1970; Studier et al. 1970; O'Farrell et al. 1971; Studier and O'Farrell 1976; Webb 1995; Webb et al. 1995). Thus, it is not surprising that the most intense drinking activity time by arid-land bats is highest during the first 1–2 h after roost emergence potentially leading to overcrowing and competative interactions among individuals and species (Cockrum and Cross 1964; Jones 1965; Adams and Hayes 2008). Notably, this pattern was not observed in tropical fruit-eating bats that showed much more evenly distributed nightly drinking activity (Brown 1968).

Climate warming and changes in water availability may have multiple unexpected effects on arid-land bats, especially reproductive females. Adams (2010) used 13 years of capture data to show that several species of myotis, with high fecundity to specific rock-crevice roosts, reduced reproductive output by as much as 50% in drought years. A breakdown of the data showed that capture frequency of lactating females was correlated with stream discharge rates, whereas frequency of gravid females did not. This aligns with the fact that largest quantities of drinking water are required for lactation because bat milk consists of nearly 76% water and water flux in lactating females is more than double that of gravid females (Kunz et al. 1983, 1994; Kurta et al. 1989a, b, 1990; McLean and Speakman 1999; Wilde et al. 1995, 1999). In a field test of lactating and nonreproductive female *M. thysanodes*, Adams and Hayes (2008) used a submersible antenna (Fig. 7.2) to record PIT-tagged individuals as they skimmed to drink at a small waterhole in Boulder County, Colorado (Fig. 7.3). Over an 11-night period, 10 lactating females visited to drink on average 21.3 times per night, whereas 6 nonreproductive females visited on average 3.7 times nightly, highlighting the increased need for water during lactation.

In other arid regions such as the Mediterranean, bats showed weak spatial landscape patterns (i.e. predictable foraging areas) during pregnancy, but during

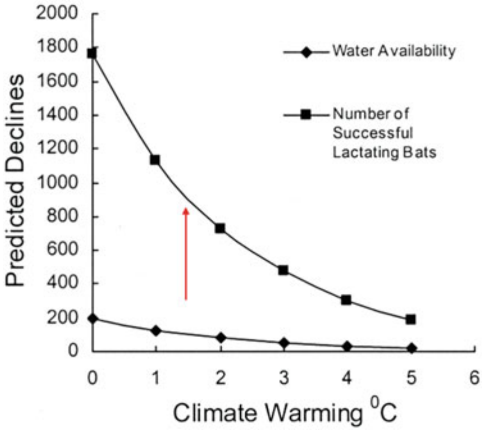

Fig. 7.3 Hypothetical decay model showing reduced water availability and consequential loss of support for milk production in female *M. thysanodes* with each degree of climate warming in Colorado. Y-axis indicates number of lactating females and liters of drinking water available. *Red arrow* indicates current degrees of warming being experienced in Boulder County, CO (from Adams and Hayes 2008)

lactation and postlactation, activity was concentrated along permanently flowing watercourses (Amorim et al. 2018). In the Badlands and Missouri River Valley of South Dakota, USA, gravid female *M. lucifugus* were active mostly at forest edges abutting grasslands, whereas lactating females were most active over water (Nelson and Gillam 2016). It remains unclear if these oatterns were driven by drinking water needs of driven by preferences for certain insects during pregnancy versus lactation. However, one study did how that female pond bats (*M. dasycneme*) in northern Poland switched from eating chironomids emerging from eutrophic lakes when gravid to larger caddisflies emerging from fast-flowing rivers during lactation (Ciechanowski et al. 2017), supporting the dietary hypothesis as associated with female reproductive state but does not rule out the drinking water hypothesis. Either way, such studies underscores how loss of water sources with increasing aridity may have multiple affects on bats as well as cascading effects on nocturnal food webs.

7.5 Quantitative Modeling of Bats, Climate Change, and Water Availability

Developing a clear understanding of how bats may respond to changing climates and water availability in arid regions requires knowledge about species distributions and populations over decades. In many cases, we lack high-quality long-term data for many bats that may be potentially impacted. Indeed, we even lack accurate distribution maps and habitat suitability parameters for many species of conservation concern globally.

In our Boulder County study area, two species of highest conservation concern (fringed myotis, *M. thysanodes* and Townsend's big-eared bat, *Corynorhinus townsendii*) are poorly understood. In Colorado, we have focused our efforts on one of these species, *M. thysanodes*, that in our area forms maternity roost sites in east- and south-facing rock crevices that reach the highest daily temperatures and therefore would predictably cause the highest evaporative water loss (Hayes and Adams 2017). Although our study area would predictably provide suitable habitat for the foreseeable future for *M. thysanodes*, we have shown that reductions in water availability near maternity roosts will have highly negative effects on reproduction and population numbers. Initially our modeling efforts focused on how the availability of drinking water would affect successful milk-production over a 21-day lactation period. Having mapped out several maternity roosts for *M. thysanodes*, we realized that the closest water sources to these rock-crevice roosts were small (3–6 m in diameter) and fed by trickling streams with decreasing flows throughout the summer months. Using data gathered from water hole visitation activity of PIT-tagged lactating vs. nonreproductive female *M. thysanodes* (see Fig. 7.2), we (Adams and Hayes 2008) developed a simple decay model of how many individuals would not have enough available for lactation as availability declined with climate warming (Fig. 7.3). To quantify how warming will affect water availability, we used Christensen et al. (2004) predictions for the Colorado River basin showing that each 1 °C increase in regional average temperature in the Southern Rocky Mountains would result in ~36% less surface water on the landscape. By averaging dimensions of three water sources located in proximity to *M. thysanodes* maternity roosts in our field areas we estimated that a 200 L water source could support about 1770 lactating *M. thysanodes* over a 21 day lactation period. We predicted a 1 °C increase in ambient temperatures and the resulting reduction in surface water availability would cause a decline from 1700 lactating females to less than 1200. As warming increased to 2 °C the number of lactating females would be <50% of the original 1770 individuals. It is currently estimated that the northern Front Range of Colorado has warmed 1.5 °C over the last two decades and our capture data collected between 1996 and 2016 show significant declines in *M. thysanodes* populations as related to increasing mean June temperatures (Adams 2018).

To envision and model future expected changes for this species, we used Monte Carlo simulations to estimate how a hypothetical population of 2000 female fringed myotis divided into four age classes (1 year olds, 2 year olds, 3 years and older, and younger than 1 year) from capture data from 1996 to 2008 would respond to eight future climate models developed by the World Research Programme's Coupled Model Intercomparison Project (CMIP5) and four representative concentration pathways for carbon emissions based on the mean annual temperature and precipitation data from our study area in Colorado over those same years (Hayes 2011; Hayes and Adams 2017).

We ran each Monte Carlo simulation 10,000 times and calculated the minimum, maximum, and average population size for year 2086. Of the eight simulation models, three populations remained approximately stable, whereas the populations of four scenarios decreased by an average of >50%, and the population of one scenario increased by almost 30%. Based on these simulations we concluded that changing climate and decreasing water availability probably eroded some forest bat populations. When these simulations were projected to the entire distributional range of *M. thysanodes* in North America, the average of all populations decreased by >90% (Fig. 7.4).

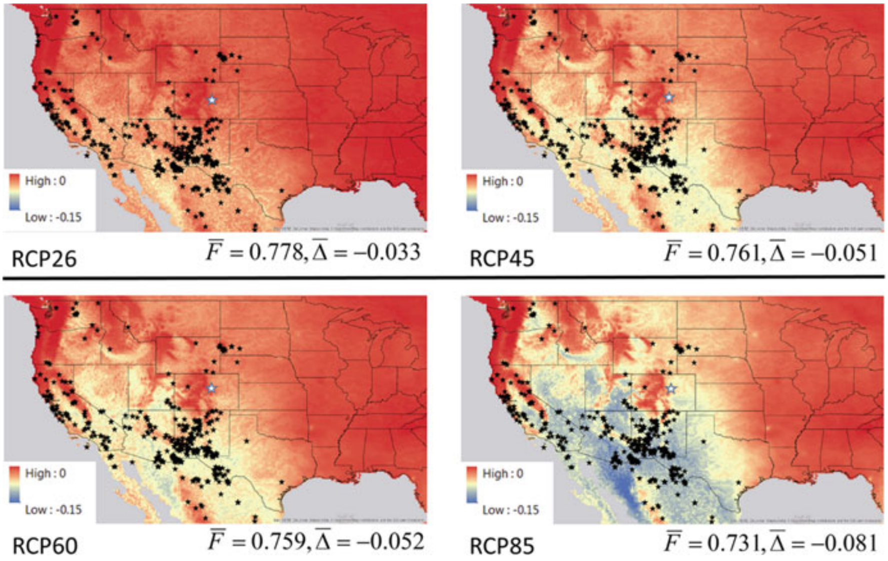

Fig. 7.4 Maps of fringed myotis (*Myotis thysanodes*) occurrence locations in western North America and projected change in adult female fertility rates using future climate projections derived from the General Ensemble Model for year 2070 using the four representative concentration pathways (RCP2.6, RCP4.5, RCP6.0, RCP8.5). Fringed myotis locations are indicated by *black stars*, and our study area near Boulder, Colorado is indicated by a *white star*. The color ramp indicates the change (Δi) in estimated fertility rate for a given cell on the map, using the estimated mean derived from the 11 future climate models when comparing the 1950 and 2000 climates to 2070 projections for the ensemble model. Darkest *red* indicates no change between the 1950 and 2000 climate and future climate projections, and darkest *blue* indicates greatest negative change. Mean projected adult fertility rates for the fringed myotis locations (F) and the mean change (Δ) from current climate conditions are also shown (from Hayes and Adams 2017)

The models presented above assumed a stable sex-ratio of 1:1 with occasional random fluctuations. However, analysis of sex ratios from capture data at our field sites over a 20-year period (1996–2015; Adams and Hayes 2018) showed clearly shifting patterns towards male-biased outcomes, especially in drought years. Including these trends by fitting logistic regression models to the sex ratio data and projecting the best-fitting model through year 2090 using the same four carbon emission scenarios (Fig. 7.5), we illustrate that all scenarios predict decreasing proportions of newborn females in future years. We have not yet incorporated sex ratio data into an age structured population dynamics model, however, it is clear that male-skewed sex ratios would place added downward pressure on *M. thysanodes* populations and perhaps other forest bats in our study area. Our quantitative modeling efforts followed the approach advocated by Turchin (2003).

Bat researchers in other arid regions also have used quantitative modeling approaches to investigate the potential impacts of changing climate conditions on bat distributions and populations. Rebelo et al. (2010) used presence-only species distribution modeling (SDM) techniques and principal components analysis to

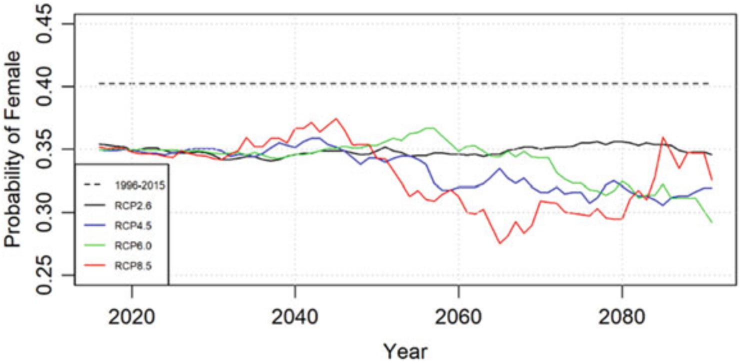

Fig. 7.5 Plots of the mean projected probability a juvenile is female for each year from 2016 to 2090, based on the logistic regression model and climate predictions using four UCAR-NCAR future climate model representative concentration pathways (RCPs) for Boulder County, Colorado (low emission, RCP 2.6; medium-low, RCP 4.5; medium-high, RCP 6.0; and high, RCP 8.5). The dashed line shows the mean probability of a captured juvenile being female using 1996–2015 capture data (0.4025)

predict the impacts of changing climate conditions on 28 European bat species. They concluded that species associated with the Mediterranean and some temperate regions may be more tolerant of increasing temperatures. Similarly, the potential impacts of changing climate conditions on species associated with the eastern Mediterranean region were analyzed, including species with distributions in Cyprus, Israel, Jordon, Lebanon, Syria, Turkey, and Egypt. By using SDM modeling and employing a maximum entropy algorithm (Maxent), they concluded that species richness is likely to decrease and that the total area occupied by bat species in this arid region will also decrease (Bilgin et al. 2012).

Amorim et al. (2018) investigated the possible influence of drought conditions and importance of permanent water resources on maintaining bat populations in the Sabor River Valley of north-eastern Portugal. By fitting correlative statistical models, including generalized linear models, Poisson, and negative binomial models to bat occurrence, species richness, and bat activity data, they concluded that permanently available water resources are critical to maintaining bat populations and species richness during periods of drought.

7.6 Can Bats Adapt to Increasing Regional Droughts?

As mentioned, hyperarid regions are noticeably low in bat species richness, whereas arid and semi-arid regions are markedly high indicating that most bat species require some access to water to persist in these environments. However, entire species, or in some cases specific populations of species, appear to have evolved, or are evolving, adaptations that benefit water retention. For example, total evaporative water loss was lower in *Eptesicus fuscus* hibernating in crevices than in those using more humid caves (Klüg-Baerwald and Brigham 2017) indicating that some individuals possessed adaptations for tolerating hibernation under more arid conditions. In other cases, entire species are known to possess higher than average kidney medullary thicknesses that correlate with urine concentration ability (Geluso 1975, 1978). However, the selective pressure in these cases may be generated by diet rather than climate. For instance, Carpenter (1969) showed that *Leptonycteris curasoae* had a larger than average renal cortex compared to insectivorous bats, presumably as an adaptation for consuming a fluid-rich, nectar diet (Rosenbaum 1970). Similarly, Studier and Wilson (1983); Studier et al. (1983) observed that frugivorous and nectarivorous bats had thinner and undivided kidney medullae compared to insectivorous bats, presumable due to their liquid-rich diets, whereas renal indices were similar across insectivorous bats regardless of inhabiting arid versus mesic habitats. Curiously, kidney adaptations for urine concentration may be more linked to diet than climate (Schondube et al. 2001), but water-concentrating kidney adaptations that evolved relative to diet may prove to be preadaptations (exaptations) for individuals living in regions transitioning towards greater aridity.

There are cases, however, where kidney adaptations for water-retention appear driven purely by daily evaporative water losses in water-limited environments, regardless of diet. Gopal (2013) found that smaller insectivorous bats in Megadermatidae and Rhinolophidae with the highest potential for daily evaporative water losses also had the highest urine concentration ability. Such adaptations appear to also have evolved in wide-ranging species of unrelated pteropodid bats such as *Rousettus aegyptiacus* (Pteropodidae) for which diet and body size is consistent throughout its range, but renal adaptation for water retention occur only in populations living in arid regions (Eshar et al. 2017). Although it is encouraging that some renal adaptations have been found and may help some bat populations as local and regional aridity increases, of continued concern is the rate of climate warming and xerification that is clealry outpacing the evolutionary rate of most bat species. In fact, even for species having some water saving adaptations, these may not be enough to avoid physiological discordance with environmental conditions. Such discordance could lead to rapid species extinctions in some areas.

Other features besides kidney adaptations may help bats mitigate evaporative water loss in arid environments, and some already exist as adaptive energy-saving mechanisms. For example, the very act of torpor lowers metabolic rate and respiration thereby significantly reducing total evaporative water loss (Studier 1970). Thus, species occupying very different habitats commonly use torpor to save energy with the side-effect of reduced total evaporative water loss potentially allowing individuals to persist in more extreme conditions. However, Muñoz-Garcia et al. (2016) found that among four bat species living in the Negev Desert, lowest total evaporative losses were recorded for those species restricted to desert habitat, intermediate for those inhabiting semi-desert habitat, and highest in wide-spread species. These data indicate that adaptations other than simply spending more time in torpor are at play.

Another mechanism known to be used by many desert mammals and birds is increasing subcutaneous lipid deposition in body areas prone to cutaneous water loss because lipids act as a barrier to evaporation (Haugen et al. 2003; Van Sant et al.

2012). Not surprisingly, this mechanism was found in the desert dwelling bat *Pipistrellus kuhli*, which lost only 80% of the cutaneous water loss of nondesert bats placed under arid conditions (Muñoz-Garcia et al. 2012). Further investigations may turn up more species and more adaptive mechanisms that reduce evaporative water loss in arid environments thereby giving hope to researchers that some species of bats may be able to tolerate rapid climate warming.

7.7 The Sex-Ratio Paradox of Climate Change

Physiological stress in female mammals caused by climate change has been cited as triggering sex ratio shifts away from 50:50 in elephant seals (*Mirounga angustirostris*), red deer (*Cervus elaphus*), domestic cows, and even human populations (see Adams and Hayes 2018 for review). Using museum specimens of eastern red bats (*Lasiurus borealis*) collected from the northern mid-Atlantic to the deep South and into the upper Midwest regions of the US, Ford et al. (2002) found that bats living in areas experiencing warmer Junes had a female sex ratio bias, whereas either males dominated or a 50:50 ratio occurred where June temperatures were cooler. Barclay (2012) analyzed long-term data on sex ratios of *E. fuscus* in Medicine Hat, Alberta, CA and discovered that in years with earlier spring-like conditions female-biased sex ratios of young occurred. Curiously, at our field sites, stress of climate warming and loss of water availability correlated with shifts towards male-biased sex ratios (Adams and Hayes 2018). Taken together, these studies indicate that there may exist a geographic pattern of shifting sex ratios in relation to climate change depending on local conditions. Several studies have directly linked diet to sex ratio outcomes in mammals, including humans (see Adams and Hayes 2018 for review) and therefore changes in availability of certain foods as climate warms may alter sex ratios in unpredictable ways.

7.8 Conclusions

Increasing xerification of already arid lands will certainly disrupt bat populations and species distributions in complex and emergent ways that are difficult to anticipate. Continued climate warming will expand arid regions globally with further spreading of hyperarid zones. In some regions, some bat species may be preadapted to increasing arid conditions that could allow for some persistence, whereas other species may experience extirpation over the next few decades. The loss of bat species in some arid regions will have large effects on biotic communities. Bats are major interactors in nocturnal food webs and link together diverse habitats and species by acting as conduits of energy, nutrient, and water distribution across tropic levels. The high metabolic rates of bats require high consumptive rates of resources

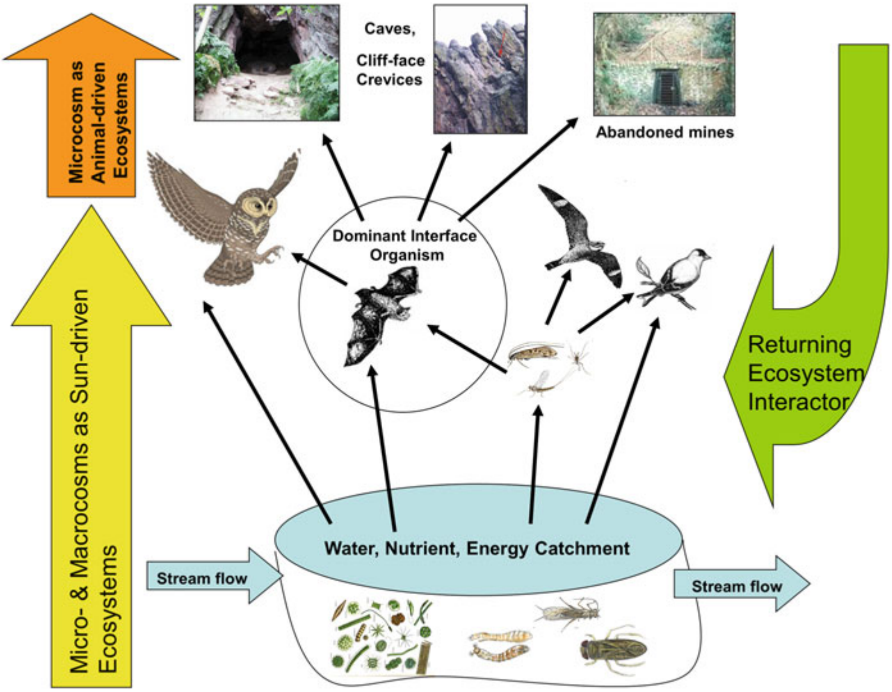

Fig. 7.6 Bats are novel interactors in food webs for which a highly simplified version is presented here. Bats interface sun-driven ecosystems with subterranean communities by the deposition of energy, nutrients, and water that support unique communities of organisms found nowhere else on Earth

and combined with their high mobility make then unique ecosystem interactors in nocturnal food webs (Fig. 7.6).

Overall modeling of the long-term data from our field areas in Colorado suggests significant declines in some bat populations and multiple indirect effects due to climate warming and increasing years of drought during the reproductive season and these patterns are corroborated by studies conducted in arid regions globally. Unequivocally, food webs for which bats play important and irreplaceable links (Kunz et al. 2011) are transitioning to new and unpredictable states. Bats are important bioindicators (Jones et al. 2009) of what will cascade through ecosystems and various trophic levels. Due to the accelerating rate of climate warming and global biodiversity losses, there is an urgent need for studies on bats as bioindicators of how complex trophic linkages forming biotic communities are being shattered and reconfigured.

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Part IV
Feeding

M. Brock Fenton

Each of the three chapters in this section focuses on feeding, but do so from different standpoints; behaviour and diet.

Ted Fleming explores his hypothesis that spatio-temporal predictability (STP) of food resources influences the search for food. He identifies major differences between Neotropical and Palaeotropical plant-visiting mammals and birds and examines them in the context of STP. The impacts are clear in species diversity, body sizes, dietary specializations and seasonal mobility. STP apparently is more prevalent in the Neotropics. The chapter is instructive because it traces the development of a coherent theme in Ted's research, which was initially presented at the 5th NASBR meeting in 1974 at Lubbock Texas, including various approaches to documenting and dissecting STP.

Juan Moreira-Hernández, Camilo Calderón-Acevedo and Nathan Muchhala consider advances in research on nectarivorous bats over the history of NASBR. About 5% of bat species eat nectar and pollen. These species occur in tropical and subtropical regions around the world. They share specializations for quick assimilation of ingested sugars, and long, specialized tongues. Neotropical species find flowers using a combination of echolocation and vision, sometimes including sensitivity to ultraviolet light. Palaeotropical species appear to rely on vision and olfaction. Some individuals travel long distances from roosts to foraging areas every day. In several chiropterophilous plants, specialized flowers and leaves reflect strong echoes and serve as beacons or nectar guides to foraging bats. Compared to Neotropical flower-visiting species, Palaeotropical taxa are much less diverse and not as well studied.

Gerry Carter, Bridget Brown, Imran Razik and Simon Ripperger examine the diversity of hosts visited by the three species of vampire bats, *Desmodus rotundus,*

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Diaemus youngi, and *Diphylla ecaudata.* Their data set was obtained from precipitin tests, stable isotope analyses, DNA sequencing, camera traps, captive experiments and field observations. The dietary diversity of vampires suggests that all three species are opportunistic. *Diphylla* shows the strongest preferences for birds, while *Diaemus* prefers birds but also feeds on mammals. *Desmodus* feeds mainly on mammals, but obtains blood from mammals, birds and reptiles. The diversity of vampires' diets varies across geographical areas and may well depend upon social information.

Chapter 8
Bats and the Ecological and Evolutionary Consequences of Resource Spatio-temporal Predictability (STP)

Theodore H. Fleming

Abstract In 1974, I presented a paper at the North American Society for Bat Research (NASBR) describing the preliminary results of an experiment aimed at testing whether fruit-eating phyllostomid bats were actively searching for fruit while commuting from their day roosts and moving between feeding areas. My hypothesis was that their fruit searching behavior depended on the spatio-temporal predictability (STP) of their fruit resources. Since then, the concept of STP has played an important role in my studies of the ecology and evolution of plant-visiting birds and mammals. Here, I briefly review these studies and conclude that resource STP has indeed been a major factor in the evolution of these animals. Major differences between Neotropical and Paleotropical plant-visiting mammals and birds in species diversity, body sizes, dietary specialization, and seasonal mobility appear to reflect historical differences in the STP of their food resources with STP apparently being higher in the neotropics than in the paleotropics. Reasons for this need further investigation but likely involve significantly different geological and climatic histories.

Keywords Phyllostomid bats · Resource spatio-temporal predictability (STP) · Frugivory · Nectarivory · *Carollia perspicillata* · *Artibeus jamaicensis* · *Leptonycteris yerbabuenae*

In 1974, I presented a paper at the symposium of the North American Society for Bat Research (NASBR) entitled "Preliminary observations on the food searching behavior of Costa Rican frugivorous bats," co-authored with Bill Sawyer, my field assistant. We described an experiment conducted that summer at Santa Rosa National Park in northwestern Costa Rica, 'the Piper pole experiment,' to determine whether fruit-eating phyllostomid bats (primarily *Carollia perspicillata* and *Artibeus jamaicensis*) maximized their rate of finding food by either combining or separating

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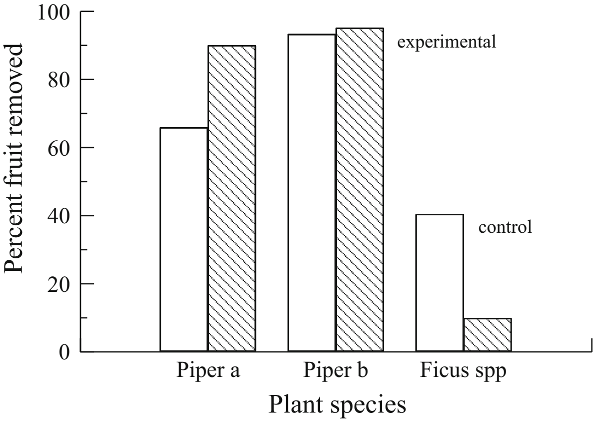
Fig. 8.1 Results of the 'Piper pole' experiments comparing the response of *Carollia perspicillata* and *Artibeus jamaicensis* for several species of fruit based on data in Fleming et al. (1977, Table 6)



commuting and search behavior. We hypothesized that the bats' choice depended on the spatio-temporal predictability (STP) of their food resources. We predicted that bats feeding on high-STP resources would combine, while those feeding on low-STP resources would separate, commuting and searching.

To test this hypothesis, we placed ripe fruit of several species that differed in their phenology and spatial distributions either on T-shaped poles embedded in the ground or on bars suspended from trees in two locations. These included conspecific resource patches (the controls) or patches away from conspecific resource patches but in bat flyways (the experimentals). We expected that bats using a combined strategy would remove as many fruit from the experimental sites as from the control sites. If the bats used a separation strategy, they would remove far less fruit from the experimental than from control sites.

Our results were dramatic. *Piper* fruits, the favorite of *Carollia*, were removed at least as often from experimental sites as from control sites. But *Ficus* (fig) fruits, favored by *Artibeus*, were removed far less often from experimental than from control sites (Fig. 8.1). These results suggested that these bat species used different foraging strategies. *Carollia* was apparently constantly on alert for *Piper* fruits when commuting to and between feeding areas whereas *Artibeus* apparently 'turned on' its fruit search behavior only in the vicinity of known fruit trees.

Working with Ray Heithaus at Santa Rosa in 1975 and 1976, we conducted many more fruit removal experiments and documented the fruiting phenology and spatial distribution patterns of several important bat fruits. We also determined bat diets and the composition of bat assemblages in and away from fruit resource patches. The results of this detailed study were published in *Ecology*, and we concluded that resource STP influenced the foraging strategies of frugivorous phyllostomids (Fleming et al. 1977).

My ideas about the foraging behavior of frugivorous phyllostomid bats were clearly influenced by discussions of optimal foraging strategies (e.g. reviewed by Pyke 1984) and focusing on the STP of food resources seemed like a logical place to begin to understand these strategies. I fully elaborated my ideas about this topic

Table 8.1 Predicted behavioral traits of frugivorous phyllostomid bats that maximize individual foraging efficiency in four idealized environments. Based on Fleming (1982, Table 3)

	Temporal dimension	
Spatial dimension	Low variability	High variability
Low variability	Specialized diet	Generalized diet
	Solitary forager	Solitary forager
	Combine commute and food search	Combine commute and food search
	Regular foraging path	Irregular foraging path
High variability	Specialized diet	Generalized diet
	Group forager	Group forager
	Separate commute and food search	Separate commute and food search
	Regular foraging path	Irregular foraging path

(Fleming 1982) and made several predictions about the behavioral traits of frugivorous bats, assuming that they were maximizing their foraging efficiency. These traits included diet breadth, foraging mode (i.e. solitary or in groups), search strategy, and regularity of foraging paths (Table 8.1).

Although the foraging behavior of only a handful of phyllostomids had been studied by 1982, we had enough information to begin to test these predictions. For example, we knew that well-studied frugivorous phyllostomids have broad diets often containing dozens of fruit species throughout their geographic ranges. We knew of no species that was a dietary specialist. But well-studied species usually had a core diet of a predictable subset of plant taxa (see below). We also knew that at least two flower-visiting species, *Phyllostomus discolor* and *Leptonycteris sanborni* (now *L. yerbabuenae*), were group foragers. We knew of no frugivores that foraged in groups. In southeastern Arizona where *L. sanborni*, was studied, its exclusive food species is *Agave palmeri*, which usually occurs in low-density, widely scattered patches—a distribution pattern that likely favors group foraging. Determining the other foraging traits in Table 8.1 required either an experimental approach (separate or combined commuting and food searching) or detailed radio-tracking studies to determine regularity of foraging paths. In 1982, such studies were non-existent (except for Fleming et al. 1977) or very scarce (e.g. Heithaus and Fleming 1978; Morrison 1978). Finally, after reviewing the behavioral ecology of three relatively well-studied frugivorous phyllostomids, I concluded that *A. jamaicensis* likely 'viewed' its resource environment on Barro Colorado Island, Panama, where it feeds heavily on *Ficus* fruits, as temporally invariable (hence a narrow diet) and spatially variable (but without group foraging). On Trinidad, *Phyllostomus hastatus* likely 'viewed' its resource environment as temporally variable (hence a relatively broad diet) and spatially invariable (resulting in stable long-term feeding areas). And *C. perspicillata* at Santa Rosa National Park likely 'viewed' its resource environment as both temporally and spatially variable (hence a relatively broad diet and seasonally changing feeding areas). In each of these three harem-polygynous species, social status also influenced foraging behavior, especially in harem males, which introduces complexity into a search for purely resource-based explanations for their foraging behavior (Fleming 1982).

Once I began to focus on resource STP in the early 1970s, I realized that it should influence many aspects of the ecology and evolution of plant-visiting bats. These aspects ranged from individual behaviors to population dynamics and eventually to community structure. In addition to features of foraging strategies (Table 8.1), I reasoned that resource STP should influence: (1) when and how often to reproduce, (2) whether or not to migrate, (3) the evolution of body size and foraging morphology as a function of food choice, and (4) patterns of coexistence and species richness within communities. I explored these topics in detail in several studies, chapters, and books published between 1982 and 2013.

In 1986, I examined ecological factors influencing the feeding strategies of frugivorous bats by addressing two basic questions: (1) To what extent is diet choice opportunistic or selective and (2) What ecological factors influence diet choice and foraging behavior (Fleming 1986)? I hypothesized (p. 205) that "within this set of fruits [of the appropriate size], diet choice merely reflects the relative abundance of suitable species." Earlier, I had suggested that most fruit-eating phyllostomids tend to have broad diets, but the question still remained, how selective is their diet in any particular locality? Is this hypothesis true?

An analysis of dietary selectivity in four to seven phyllostomid species at three sites in Costa Rica revealed that selectivity was common, allowing me to identify the highly selected core fruit taxa in the diets of species of *Carollia*, *Sturnira*, and *Artibeus*. These core taxa included *Piper*, *Piper* and *Solanum*, and *Ficus* and *Cecropia*, respectively. This dietary selectivity did not support my initial hypothesis. A major reason for this selectivity appeared to be the high spatio-temporal availability (i.e. STP) of these fruit taxa, which tend to be species-rich in many neotropical habitats and, collectively, tend to produce fruit throughout the year.

I also reported an interesting tradeoff between the nutritional quality of these core fruit taxa and their nightly per-plant availability. Ripe fruits of *Piper* and *Solanum* tend to be rich in protein and low in fiber, and they are produced in low numbers per plant each night for weeks. In contrast, *Ficus* fruits are rich in fiber and low in protein and are produced in large numbers per plant each night for short periods of time. As a consequence of their fiber-rich diets, *Artibeus* bats and its relatives have more specialized skull morphology than species of *Carollia* and *Sturnira*, and they consume individual fruits much more slowly (e.g. Bonaccorso and Gush 1987; Dumont et al. 2012).

Resource STP also strongly influences the reproductive biology of phyllostomid bats. Because the availability of their fruit (or flower) resources often (usually) varies in a seasonally predictable fashion, many plant-visiting phyllostomids have bimodally polyestrous reproductive cycles that coincide with the rhythms of their food resources. As a result, many adult females produce two young each year. In contrast, most animalivorous phyllostomids and their close relatives (i.e. mormoopids) and a few nectar-feeders are monestrous and produce a single pup annually (Barclay and Fleming 2020).

Migration, at least over distances of more than a few dozen kilometers, is uncommon in phyllostomids and apparently occurs only in a few plant-visiting species (Fleming and Eby 2003). As in the case of reproductive cycles, migration, or its absence, seems to depend on the STP of food resources. For frugivores such as *C. perspicillata* and *A. jamaicensis*, among other species, seasonally based between-habitat movements involving resource tracking sometimes occur (reviewed in Fleming 1992). There is, however, no evidence of long-distance migrations in these bats. In contrast, several species of the nectar-, pollen-, and fruit-eating genus *Leptonycteris* (Phyllostomidae, Glossophaginae) make long distance migrations. In *L. yerbabuenae*, for example, many females mate in southwestern Mexico in November–December and then fly about 1000 km north to form maternity colonies containing thousands of individuals. These colonies are in caves and mines in the Sonoran Desert of northwestern Mexico and southwestern Arizona where females give birth to a single pup beginning in mid-May. The primary driver behind this migration appears to be a predictable and copious spring flowering season followed by an equally copious summer fruiting season of several species of Sonoran Desert columnar cacti. In the spring, the per-capita resource density in the Sonoran Desert is likely to be much higher than the per-capita resource density in tropical dry forests in southern Mexico (Fleming et al. 2001). The flowering behavior of a predictable suite of lowland columnar cacti provides nectar and pollen that fuels the spring migration (Fleming et al. 1993). *Leptonycteris yerbabuenae*'s sister species, *L. curasoae*, is also migratory in the arid regions of northern Venezuela, Colombia, and islands in the Dutch West Indies (Fleming and Nassar 2002; Simal et al. 2015).

In 1992 I wrote an essay in which I expanded my focus to include nectar-feeding as well as fruit-eating birds and bats and compared many of their biological traits with those of their insectivorous relatives (Fleming 1992). My working hypothesis was that animals and their life histories should closely track their resources to maximize their lifetime fitness. In addition to reproduction and foraging behavior, resource STP should also influence social organization and mating system. I also hypothesized that because of differences in the STP of their food resources, life histories of plant-visitors should differ significantly from those of their insectivorous relatives. In addition, I postulated that body size should have an important effect on how animals experience their environment. Small species are likely to live in more variable (potentially less predictable) worlds than large species. I further predicted that because of their potentially greater mobility, aerial species such as birds and bats likely live in less variable worlds than non-aerial species. [Please note that up to 1992, I had used STP to denote spatio-temporal *patchiness*, the inverse of spatio-temporal *predictability*. I have used the latter meaning in subsequent publications, including this one.]

As I predicted, the results of this extensive review revealed that many aspects of the life histories of nectar- and fruit-eating birds and bats are indeed sensitive to, and have likely evolved in response to, the STP of their food resources. I also noted that life histories of these animals often differ substantially from those of their insectivorous relatives. Population densities, for example, are usually much higher and seasonally more variable in frugivores than in insectivores. Especially striking is the widespread occurrence of territorial behavior during the breeding season in many insectivorous birds resulting from defense of mates and food resources. Except for many hummingbirds and some pteropidid bats, resource-based territoriality is absent in most plant-visiting birds and bats.

In 1987 and beyond, I began to explore the consequences of resource STP for the structure and biological features of communities of tropical plant-visiting birds and mammals. For example, graduate students George Whitesides and Randy Breitwisch and I compared and contrasted the structure of communities of fruit-eating birds and mammals in the Neotropics and Paleotropics (Fleming et al. 1987). We first compared the species and generic richness of three biogeographic regions (Neotropics, Africa, and mainland Southeast Asia) and noted that the Neotropics generally had higher generic and species richness in birds and mammals. Correcting for differences in their geographic areas, however, somewhat reduced these differences. More importantly for this paper, the three areas differed strikingly in: (1) the average body sizes of their frugivores and (2) their individual use of space on an annual basis. Compared with Africa, and especially Southeast Asia, Neotropical avian and mammalian frugivores were significantly smaller in size, were less-often strongly terrestrial, and were more sedentary.

Substantial geographic differences also exist at the community level (Fleming et al. 1987). Species richness in communities of fruit-eating birds and mammals is substantially higher in the Neotropics, and dietary overlap among birds, bats, and primates and the occurrence of nomadism is lower. After reviewing potential historical and ecological processes that might have produced these patterns, we concluded that resource STP, perhaps reflecting climatic histories rather than geological histories (*sensu stricto*), has probably played an important role in these differences. High resource STP favors the evolution of feeding specialization resulting in lower dietary overlap, sedentary lifestyles, and smaller body sizes. Low STP, in contrast, favors feeding generalization, higher dietary overlap, and greater mobility via larger body size for tracking highly patchy resources. After reviewing fruiting patterns in different biogeographic regions, we concluded that although they varied in space and time, fruit (and flower) resources in the Neotropics have been significantly more predictable historically than those in Southeast Asia with Africa being intermediate (also see Van Schaik and Pfannes 2005).

As a follow-up to the frugivore-based review of Fleming et al. (1987), my student Nathan Muchhala and I explored in detail the consequences of evolutionary history and resource STP on the structure and biological features of communities of Neotropical and Paleotropical nectar-feeding birds and bats and found many of the same ecological and evolutionary trends reported for frugivores (Fleming and Muchhala 2008). Compared with assemblages of Paleotropical vertebrate nectarivores, Neotropical assemblages are characterized by a higher diversity of more morphologically and dietarily specialized nectar-feeders as well as greater ecological and taxonomic diversity of their food plants. New World nectarivores such as hummingbirds and glossophagine bats are small and can hover at flowers whereas Old World nectarivores such as sunbirds, honeyeaters, and pteropodid bats are larger and usually do not hover at flowers. We also found lower dietary overlap

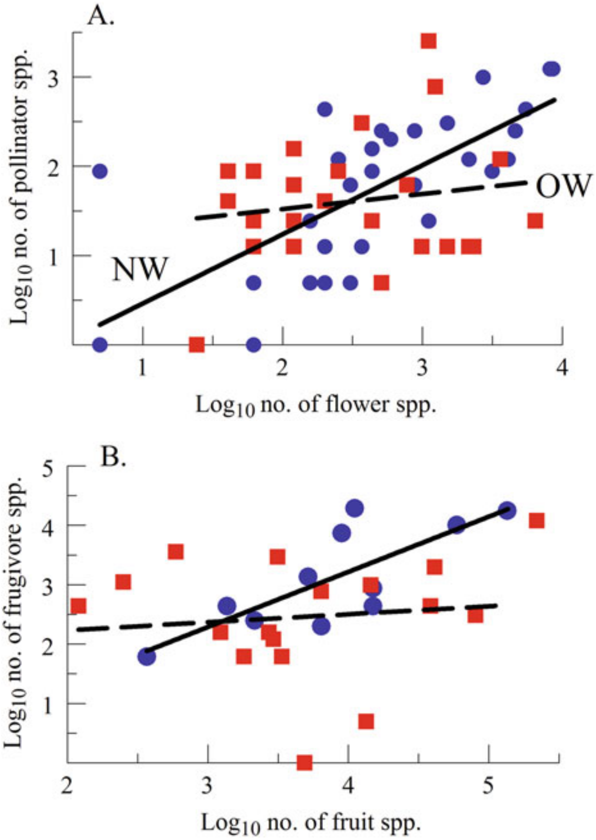


Fig. 8.2 Relationship between the number of species nectar-feeding (**a**) and fruit-eating (**b**) birds and bats (combined) and species of their food species in 87 New World (NW, *filled circles*) and Old World (OW, *filled squares*) communities. From Fleming and Kress (2013, Figure 2.14 with permission). Statistical results are in Fleming (2005)

between Neotropical nectarivorous birds and bats compared to their paleotropical ecological counterparts. Finally, a review of the morphology and ecological diversity of their food plants revealed that many neotropical plants had more specialized morphology and a greater diversity of life forms than many paleotropical plants. We concluded that all of these differences are consistent with greater resource STP in the New World than in the Old World, especially in Southeast Asia.

To continue my community-level biogeographic comparisons, I analyzed the relationship between the number of flower and fruit species and their bird and bat pollen- or seed-dispersing species in 87 tropical and subtropical communities (Fleming 2005). I tested the prediction that this relationship differs between the Neotropics and Paleotropics. Knowing that these plant-animal relationships tend to be more specialized in the Neotropics than in the Paleotropics, I expected to find significant hemispheric differences in these statistical relationships. My results supported my expectation: the number of species of vertebrate pollinators and frugivores was strongly correlated with the number of species of their flowers and fruits in the Neotropics but not in the Paleotropics (Fig. 8.2). In the New World, it takes about three species of flowers or fruit to support one species of nectar-feeder or frugivore.

This assembly rule (*sensu* Keddy and Weiher 1999) apparently does not exist in the Old World. To explain these hemispheric differences, I again proposed that resource STP has been historically greater in the Neotropics than in the Paleotropics. This has resulted in more specialized relationships between neotropical nectarivores and frugivores and their food plants.

Finally, as a capstone to my research career, between 2003 and 2013 I collaborated with botanist W. John Kress on a book ‘The Ornaments of Life: Coevolution and Conservation in the Tropics’ in which we examined the ecology, evolution, and coevolution of tropical plant-visiting birds and mammals, especially bats and primates, with their food plants from a phylogenetic perspective (Fleming and Kress 2013). After reviewing the taxonomic diversity of plant-visiting birds and mammals and their food plants regionally and at the community level, we summarized the nutritional and phenological characteristics of their flowers and fruit with a special emphasis on their STP. We then thoroughly examined micro- and macroevolutionary aspects of plant-animal pollinator and frugivore mutualisms before discussing the evolution of communities of these mutualists in space and time. Overall, our synthesis highlighted in broad-brush fashion the strong influence of geological history, biogeography, and climate change on the evolution and coevolution of plant-visiting vertebrates and their food plants. The striking biogeographic differences in the taxonomic diversity and degree of specialization in the plant-animal interactions that we see today have had a long evolutionary history over most of the Cenozoic Era. Again, these differences imply that the biogeographic differences in resource STP that we see today have had a long evolutionary history.

What’s been the response to these publications? How widely cited are they, and how have they influenced our view of the importance of resource STP on the ecology and evolution of plant-visiting vertebrates? Citation history is one way to view the impact of these publications on subsequent research. Given that these publications span over four decades and appear both as journal articles ($n = 4$) and book chapters or books ($n = 4$), I would expect their citation histories to be quite variable. Older (i.e. pre-1990) journal papers are likely to be more widely cited than more recent ones, and journal articles are likely to be more widely cited than book chapters or books (because the former are more accessible and easily searched for electronically than the latter).

The actual citation histories of these publications do not always support these expectations (Fig. 8.3). Our review in Annual Reviews in Ecology and Systematics (Fleming et al. 1987), which I’ve classified as a journal article, is by far the most cited of these publications, likely because it was aimed at a broader audience than just bat researchers. Many tropical ecologists have told me that they have read and been inspired by this paper. The 1982 and 1986 book chapters have also been relatively widely cited, but I would guess mostly by bat biologists. To see whether this is true, I used Google Scholar to determine the main subject of the top 20 articles and books citing Fleming (1982) and Fleming et al. (1987). I scored these citations as dealing primarily with bats or not. I found that for Fleming (1982), 18/20 (90%) citations dealt primarily with bats. For Fleming et al. (1987), 2/20 (10%) citations dealt primarily with bats. The post-1990 articles (and one book) do not yet have

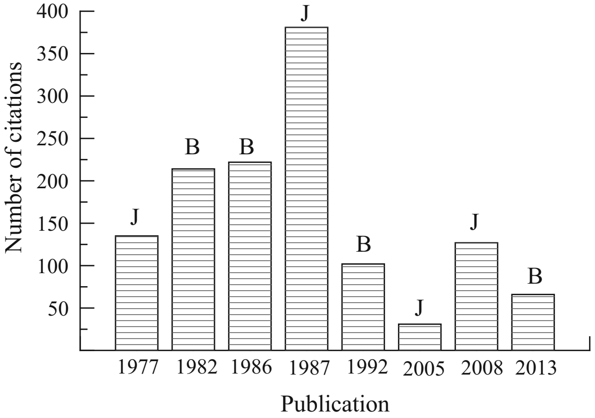


Fig. 8.3 Citation history (as of June 2019) of eight of my papers, chapters, and books. *B* book or book chapter, *J* journal article

much of a citation history, even though Fleming and Kress (2013) has been viewed as an important milestone in discussions of the ecology and evolution of tropical organisms (Jordano 2014). As an aside, my editors at the University of Chicago Press have indicated that academic book sales are currently on the decline so that books such as 'Ornaments' will likely end up on many fewer bookshelves than in the past. Supporting this, Nathan Muchhala has told me that very few of his age-cohort of academic colleagues buy books anymore. In contrast, most colleagues in my age-cohort often bought books for their personal libraries.

I suspect that the idea that resource STP has influenced the ecology and evolution of many kinds of organisms now appears to be well-accepted. In an attempt to confirm this, I conducted a Web of Science search using 'spatio-temporal predictability and resources' as my search string from 1985 to 2019. Interestingly, I found no references that explicitly used this phrase in its keywords from 1985 to 1999 and only six references between 2000 and 2019 that did. These citations dealt with animal movement patterns, reproduction, and the evolution of life histories—important topics that are highly likely to be sensitive to resource fluctuations (e.g. Berger-Tal and Bar-David 2015; Cayuela et al. 2016; Clulow et al. 2011). More fruitful were Web of Science or Google Scholar searches of citations of Fleming (1982, 1986), and Fleming et al. (1987). Banack's (1998) study of diet selection in two pteropodid bats (*Pteropus samoensis* and *P. tonganus*) on American Samoa was relevant to STP. She found that, unlike mainland plant-visiting bats, the diets of these species did not contain a set of core plant resources (fruits and flowers). Rather, the diets of these bats simply tracked seasonal availability of food resources. She attributed the lack of a core set of plant resources in island-dwelling pteropodid bats to the low STP and low species diversity of potential food sources on islands that are frequently struck by strong cyclones. Tan et al. (1998) studied the diet of the pteropodid *Cynopterus brachyotis* in Malaysia and reported that these bats preferred to feed on fruits with long fruiting seasons. They did not explicitly identify resource STP as a major factor in food choice, but their results imply that it is. In an analysis of cranial structure of plant-visiting phyllostomid and pteropodid bats, Dumont (2004) found higher cranial diversity in New World bats than in Old World bats. She suggested that these results reflect greater feeding selectivity and specialization and reduced food niche overlap in the Neotropics compared with the Paleotropics, perhaps as a result of historically greater resource STP in the New World. Finally, several recent broad-brush surveys of the community structure of plant-visiting Neotropical and Paleotropical birds and mammals confirm that Neotropical systems are currently more diverse and specialized than Paleotropical systems, but they don't explicitly state that geographic differences in resource STP are major drivers of these differences (e.g. Dehling et al. 2014; Muñoz et al. 2019; Zanata et al. 2017).

Aside from its theoretical importance, resource STP also has important conservation implications because it influences dietary selectivity, among many other biological features, in phyllostomid bats. To the extent that the persistence of core plant resources (e.g. species of *Piper*, *Solanum*, and *Ficus* for frugivorous phyllostomids) is threatened by deforestation and habitat fragmentation, species that rely heavily on them are obviously also threatened. Similarly, destruction or heavy disruption of the nectar corridors formed by columnar cacti and paniculate agaves in western Mexico will threaten successful migration in *Leptonycteris* bats (Fleming 2004). Frugivores such as species of *Carollia*, *Sturnira*, and *Artibeus* play important roles in the regeneration of Neotropical forests (Muscarella and Fleming 2007), and species of *Leptonycteris* are important pollinators of columnar cacti and paniculate agaves (Fleming et al. 2001; Fleming and Nassar 2002). Loss of these species would have a strong negative effect on the reproductive success and persistence of their food plants.

The concept of the spatio-temporal predictability of food resources has played a major role in my thinking and research about the ecology of plant-visiting phyllostomid bats. It has given me important insights into many aspects of phyllostomid biology as well as the biology and ecology of other plant-visiting vertebrates, including birds and primates. My STP-focused research began in the summer of 1974 when we conducted our first 'Pipe pole' experiments and continued for nearly 40 years. During that time, my research focus expanded from considering the nightly foraging behavior of *C. perspicillata* and *A. jamaicensis* to the structure and function of assemblages of plant-visiting vertebrates in space and time. It's been a grand journey—one that has benefited from approaching most of my research questions from a strong conceptual framework based on evolution by natural selection and its consequences.

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Chapter 9

Fur, Wings, and Flowers: Development and Progress on Nectarivorous Bat Research in the Last 50 Years

Juan I. Moreira-Hernández, Camilo A. Calderón-Acevedo, and Nathan Muchhala

Abstract Nectarivory or the habit of feeding on nectar and pollen from flowers occurs in nearly 5% of all bat species. Nectarivorous bats are found in tropical and subtropical regions around the world and possess a suit of adaptations to find flowers, extract nectar, metabolize sugars and nutrients from nectar and pollen, and fly long distances to find enough food to meet their high metabolic demands. Quick assimilation of ingested sugars allows for fast, powered, and hovering flight. With their long-specialized tongues, bats can rapidly probe flowers and extract nectar efficiently. To find flowers in dark environments, bats rely on their elaborate echolocation system, keen sense of smell, and good vision, which is even sensitive to ultraviolet light in some cases. Some species frequently fly long-distances in agricultural landscapes or following regular migration routes, thus promoting gene flow between plant populations. In addition, nectarivorous bats provide pollination services for hundreds of economically important plant species. The intricate relationships between bats and flowers also provide educational opportunities to raise awareness about the value of bats to our diverse societies and ecosystems, fostering solutions to the conservation challenges faced by bat populations. The North American Society for Bat Research has been an important forum where much of this body

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of work has been presented during the last five decades, and we hope that it will continue to play this role in the future.

Keywords Bat pollination · Chiropterophily · Glossophaginae · Lonchophyllinae · Pteropodidae · Nectarivory

9.1 Introduction

In tropical and subtropical ecosystems bats have adopted multiple dietary niches other than insectivory. Nectarivory, feeding from nectar of angiosperm flowers, has evolved independently in distantly related groups of bats from both Old and New World. Although nectarivory in bats has been known since at least the late nineteenth century, the last several decades have seen increased research in this area. Here, we review much of this work, focusing on studies presented during the 50 years since the first meeting of the North American Society for Bat Research (NASBR).

Bats in the families Pteropodidae and Phyllostomidae account for most nectarivory in Chiroptera (Fig. 9.1). There are approximately 67 bat species from 25 genera ecologically and morphologically specialized for eating nectar (Muchhala and Tschapka 2020; Fleming et al. 2009). This is about 5% of the approximately 1400 species of bats known to date. Fifty-two species in 19 genera of specialized nectarivorous phyllostomids belong to the subfamilies Glossophaginae and Lonchophyllinae. In contrast, specialized nectarivorous pteropodids include 15 species in 6 genera in predominantly frugivorous lineages from three different subfamilies (Pteropodinae, Rousettinae, and Epomophorinae). Species from the two families share a suit of common morphological characteristics adapted for nectarivory. These include narrow and elongated rostra to probe flowers, reduced dentition, and a long tongue adapted for quick nectar extraction (Birt et al. 1997; Tschapka et al. 2015). However, dozens of species from other primarily frugivorous genera in these two families opportunistically visit flowers and eat nectar and pollen either seasonally or on a regular basis (e.g. *Phyllostomus*, *Carollia*, *Sturnira*, *Artibeus* in Phyllostomidae; *Pteropus*, *Eidolon*, *Rousettus*, *Cynopterus* in Pteropodidae; Fleming et al. 2009; Fig. 9.1). There also are two notable cases of nectarivory in the insectivorous families Vespertilionidae (*Antrozous pallidus*; Frick et al. 2009) and Mystacinidae (*Mystacina tuberculata*; Fleming et al. 2009). We consider these frugivorous/nectarivorous and insectivorous/nectarivorous bat groups as opportunistic nectarivores, because nectar and pollen are not their primary food sources. Whether specialized or opportunistic, nectarivorous bats play a major ecological role as pollinators of hundreds of plant species around the world (Fleming et al. 2009), many of considerable socioeconomic importance (Fujita and Tuttle 1991; Trejo-Salazar et al. 2016).

Here we focus on the development and progress of research on nectarivorous bats worldwide. First, we briefly discuss the early descriptions of bat pollination. Second,

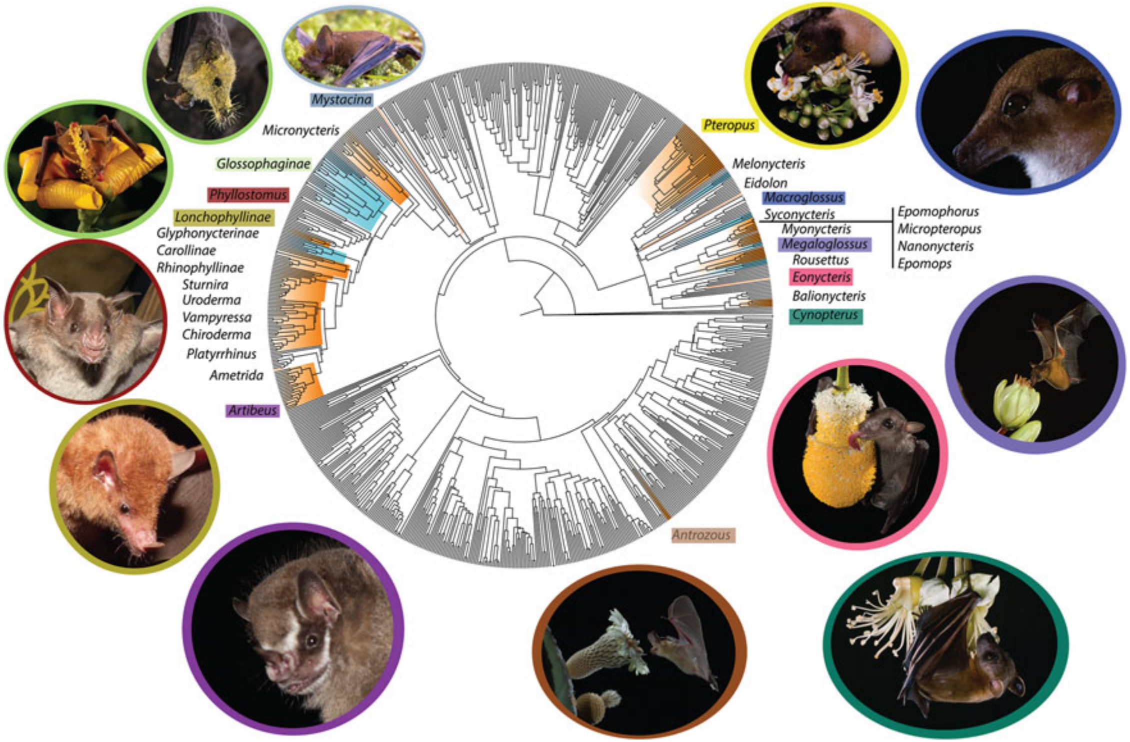

Fig. 9.1 Clades of specialized (*blue*) and opportunistic (*orange*) nectar-feeding bats superimposed on the phylogenetic tree of Chiroptera. All highlighted branches on the *left side* of the tree represent clades belonging to the New World leaf-nosed bat family (Phyllostomidae) except for the New Zealand endemic *Mystacina* (Mystacinidae). Likewise, the colored taxa on the *right side* of the tree belong to the Old World flying fox family (Pteropodidae), with the exception of the opportunistic nectar-feeding North American vesper bat *Antrozous* (Vespertilionidae). Some color-coded representative taxa are also illustrated around the tree. Photo credits: *Mystacina* by S. Parsons; *Phyllostomus* and *Artibeus* by C. Calderón-Acevedo; Lonchophyllinae by N. Muchhala; and all remaining photographs to ©MerlinTuttle.org

we show the emergence of experimental studies on nectarivorous bats that coincide with the start of NASBR. Third, we discuss those key contributions and study systems fundamental to our understanding of this aspect of bat biology. We focus on four themes: (1) physiology of nectar- and pollen-feeding; (2) sensory biology (echolocation, vision, and olfaction); (3) foraging and spatial ecology; and (4) socio-economic aspects of bat pollination and conservation. We then conclude by providing fruitful future research directions and highlighting important gaps in our knowledge.

9.2 Early Descriptions of Bat Pollination

The first publications that established the validity of the bat pollination syndrome (chiropterophily) were based on multiple records accrued since the late 1800s (van der Pijl 1961; Vogel 1969). Chiropterophilous flowers are characterized by nocturnal anthesis, predominantly dull or drab flower colors, strong musty smell, large and sturdy inflorescences and/or flower structures, copious production of pollen and hexose-rich nectar, and exposed flowers or inflorescences often growing along the main trunk and branches or suspended from long stalks away from background foliage to allow easy access by bats. Following these seminal publications, the first wave of experimental studies began in the next decade to investigate the ecological and evolutionary consequences of nectarivory in bats (see Fleming et al. 2009; Muchhala and Tschapka 2020).

9.3 Impact of NASBR on Nectarivorous Bat Research

Some of the earlier developments in research on bat-flower interactions occurred at NASBR. The first meeting in 1970 at Tucson, Arizona, had two papers focused on nectarivorous bats: population status of *Leptonycteris nivalis* in Big Bend National Park, Texas (Easterla 1972) and diet of *Leptonycteris yerbabuenae* on nectar and pollen from several flowering plants in its desert habitat (Howell 1974a). In the decades since, the number of presentations on nectarivorous bats presented at NASBR meetings has increased. To track the recent history of nectarivorous bat research, we perused the programs of 49 years of NASBR meetings (1970–2019). We selected titles that explicitly dealt with bat pollination or with aspects of bat biology linked to the nectarivorous habit. We did not include taxonomic or systematic papers, unless they explicitly addressed aspects of the ecology and evolution of bat nectarivory (e.g. evolution of feeding habits in Phyllostomidae). The resulting full list of presentations and their respective peer-reviewed publications is available online as Electronic Supplementary Material.

We found 287 oral and poster presentations on nectarivore biology at NASBR (Fig. 9.2), which have generated 124 peer-reviewed publications (as of December

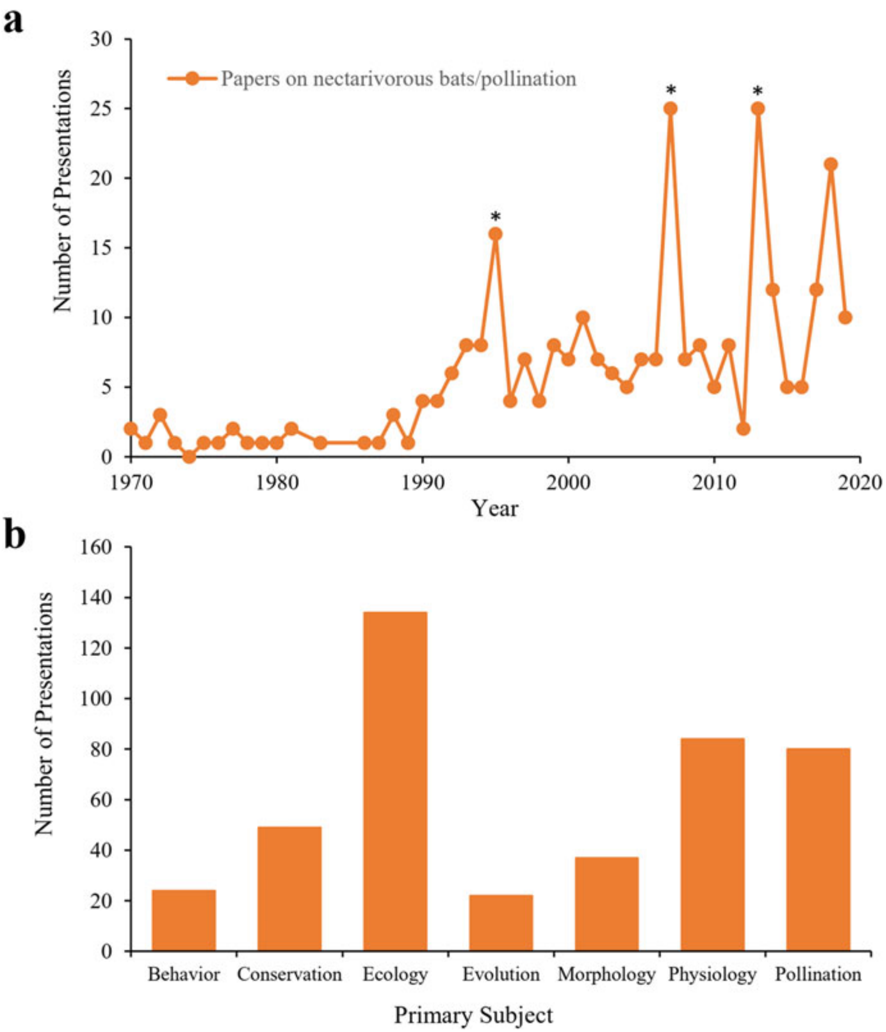

Fig. 9.2 (**a**) Number of poster and oral presentations on nectarivorous bat biology during North American Society for Bat Research (NASBR) meetings per year from 1970 to 2018. Joint NASBR meetings with the International Bat Research Conference showed a greater number of presentations and are indicated with an *asterisk* (Boston, USA 1995; Mérida, México 2007; and San José, Costa Rica 2013). (**b**) Number of poster and oral presentations on nectarivorous bat biology during NASBR meetings from 1970 to 2018 categorized by primary subject

2019). On three occasions when NASBR met with the International Bat Research Conference (Boston, USA 1995, Mérida, México 2007, San José, Costa Rica 2013), there were more oral and poster presentations about nectarivorous bat and pollination research than usual (Fig. 9.2a). There was a similar spike in the numbers of papers presented during the 2018 meeting in Puerto Vallarta, México, reflecting many Mexican student presenters. The most common topics were ecology (e.g. foraging habits, diet, migration), followed by physiology (e.g. energetics, digestion), pollination (e.g. flower visitation, pollen transfer), and, more recently, conservation (e.g. population status, pollination services to crops; Fig. 9.2b).

We identified 74 nectarivorous bat species mentioned by papers presented at NASBR. These belong to 36 genera and all 4 bat families where nectarivory occurs. They include 29 species in 11 genera from the Old World, of which 5 species in 4 genera are specialists and 24 species in 7 genera are generalists. From the New World, 45 species have been studied, representing 25 genera, comprising 30 species of generalists in 15 genera and 15 specialists from 10 genera. Table 9.1 shows the 15 most common nectarivorous bat species from the New and Old World that were mentioned in presentations at NASBR, with New World nectarivorous phyllostomids better represented than Old World species. Those from the United States and Mexico have been the most studied and most of our examples (>80%) in the next sections are derived from presentations at NASBR, highlighting the importance of this symposium in stimulating nectarivorous bat research.

9.4 Physiology of Nectar- and Pollen-Feeding

Feeding adaptations for nectarivory encompass a set of characters that help bats use pollen and nectar as primary food sources. Finding food may mean traveling long distances, which nectarivorous bats do aided by physiological adaptations for effective energy expenditure, powering up to 80% of their hovering flight with recently ingested sugars (Fleming et al. 1993; Voigt and Winter 1999). One of the early studies on the physiological consequences of nectarivory found that nitrogen-rich pollen constitutes an important supplement to the carbohydrate-rich diet of nectarivorous bats (Howell 1974a). Pollen from bat-pollinated plants germinates in the bats' gut, which increases the amount of nutrients liberated from the grains that bats can absorb. Moreover, pollen from chiropterophilous plants has a higher concentration of nitrogen than closely related plant species pollinated by other animals, suggesting that this high nitrogen content may represent an evolutionary adaptation to encourage bat visitation.

Hovering flight has evolved in very disparate groups that rely primarily on floral resources, such as moths, hummingbirds, and specialized nectarivorous bats (Voigt and Winter 1999; Ingersoll et al. 2018). In vertebrates, this adaptation is energetically expensive and constrained by the aerobic capacity of the flight muscles that must provide lift equal to their body weight. Nectarivorous bats and hummingbirds accomplish this through physiological adaptations for rapid oxygen transport and metabolic breakdown of sugars and long-chain fatty acids in the flight muscles (Voigt and Winter 1999). This energy feeds vigorous flapping movements that generate air vortexes above and below the wings, which help the animal stay airborne. A detailed comparative study of hummingbirds and bats showed that both groups require a similar total amount of aerodynamic power per unit of mass

Table 9.1 The top 15 most-frequently studied species of specialized and opportunistic nectarivorous bats from the New and Old World based on papers presented at the North American Society for Bat Research (NASBR) meetings from 1970 to 2018

New world	Species	# Papers	Old world	Species	# Papers
Phyllostomidae			Pteropodidae		
Glossophaginae	***Leptonycteris yerbabuenae****	**56**		***Macroglossus minimus***	**8**
	Glossophaga soricina*	**32**		***Syconycteris australis***	**8**
	Leptonycteris nivalis*	**27**		***Eonycteris spelaea***	**7**
	Anoura geoffroyi*	**16**		*Pteropus samoensis*	5
	Choeronycteris mexicana*	**16**		*Pteropus vampyrus*	5
	Anoura caudifer	**9**		*Cynopterus brachyotis*	4
	Monophyllus redmani	**9**		*Pteropus poliocephalus*	4
	Erophylla sezekorni	**8**		***Melonycteris melanops***	**3**
	Glossophaga longirostris	**6**		*Pteropus mariannus*	3
	Leptonycteris curasoae	**6**		*Pteropus rufus*	3
	Phyllonycteris poeyi	**6**		*Rousettus aegyptiacus*	3
	Glossophaga commissarisi	**5**		*Rousettus amplexicaudatus*	3
Lonchophyllinae	***Lonchophylla robusta***	**7**		*Cynopterus sphinx*	2
Stenodermatinae	*Artibeus jamaicensis**	5		***Macroglossus sobrinus***	**2**
Vespertilionidae	*Antrozous pallidus**	**5**		*Pteropus hypomelanus*	2

Specialized nectarivorous bats are shown in bold. New World species that occur in the United States and Mexico are indicated by an asterisk

(Ingersoll et al. 2018), but they differ in the mechanism to produce lift. Hummingbirds generate this force through very fast mostly horizontal wingbeats, whereas bats drag their proportionally longer wings during extended downstrokes (Ingersoll et al. 2018). The convergence towards hovering flight among hummingbirds and bats is striking, given its high energetic costs, and implies long-term availability of abundant and spatially predictable nectar resources during the evolution of these nectarivorous taxa in the Neotropics.

Feeding habits and physiological responses have been studied in some Old World pteropodids. A good example is the specialist *Syconycteris australis*, which is highly limited by the availability of nitrogen in its diet (Law 1992). Compared to opportunistic nectarivores, such as flying foxes (*Pteropus* spp.), *S. australis* exhibits slower pollen passage time in the gut that encourages pollen germination and an efficient nitrogen uptake to meet its nightly nitrogen needs.

Some of the most remarkable adaptations of nectarivorous bats are their feeding mechanisms and the role of the tongue in facilitating rapid nectar extraction (Birt et al. 1997; Tschapka et al. 2015). Although all nectarivorous bats have elongated tongues to reach deep into flowers (Birt et al. 1997; Muchhala and Tschapka 2020), different groups exhibit distinct feeding behaviors and tongue morphology. Glossophagines have long tongues with hair-like erectile papillae at the tip, and feed using fast lapping movements during which the papillae form rows that encircle nectar before the retracting tongue carries it into the mouth (Muchhala and Tschapka 2020). In contrast, lonchophyllines have mostly hairless tongues with lateral grooves along the length where nectar is drawn towards the mouth through a combination of capillary action and dynamic tongue pumping (Tschapka et al. 2015). Lonchophyllines must keep their tongues fully extended and immersed in the nectar during this process (Tschapka et al. 2015). In specialized nectarivorous pteropodids (e.g. *Eonycteris spelaea*), tongues are often long, protractible, and covered in long filiform papillae (Birt et al. 1997). In contrast, tongues of generalist pteropodids (e.g. *Pteropus*, *Epomophorus*) are not as long, but are still longer than other frugivorous pteropodids and are covered by different types of papillae that facilitate feeding on both nectar and fruit. The physiological adaptations of nectarivorous bats remain relatively underexplored, but are crucial to understanding their ecology and evolution. This baseline information is in turn necessary to predict how nectarivorous bat populations may respond to rapid environmental change and other anthropogenic threats. For example, climate change effects on flowering phenology may decrease food availability and impose heavy physiological constraints on those bat species unable to migrate or switch to alternative food resources.

9.5 Behavior and Sensory Biology

Nectarivorous bats have a suite of behavioral and sensory adaptations to find flowers. In phyllostomids and pteropodids, foraging involves integrating multiple sensory systems in response to diverse floral stimuli. In both groups, large scale orientation is based on a combination of olfactory and visual cues, which phyllostomids further supplement with acoustic cues (Egert-Berg et al. 2018; Muchhala and Tschapka 2020). Floral volatiles containing dimethyl sulfide and other sulfuric compounds have evolved convergently in several New World bat-pollinated plant species (Pettersson et al. 2004). In contrast, Old World bat-pollinated plants seem to lack any consistent scent bouquet pattern (Pettersson et al. 2004), and experimental tests have demonstrated that dimethyl sulfide is not preferred by pteropodid bats (Carter and Stewart 2015). Notably, the flowers from Old World populations of the pantropical bat-pollinated canopy tree *Ceiba pentandra* do not emit dimethyl sulfide (Pettersson et al. 2004), whereas its Neotropical populations do. These findings suggest that Old and New World nectarivorous bats exert different selection pressures on the floral scents of the plant species they pollinate. Research devoted to elucidate the timeline and mechanisms explaining this divergence would be useful to understand the evolution of floral scents mediated by bat pollinators.

The importance of echolocation for foraging by specialized nectarivorous Phyllostomidae was first observed decades ago. Glossophagine and lonchophylline bats use typical low-intensity, short-duration, broadband, multi-harmonic, and frequency-modulated echolocation calls that are efficient for orientation in cluttered environments (Muchhala and Tschapka 2020). However, different nectarivorous species rely on floral resources to varying degrees, and some even shift almost entirely to insectivory or frugivory for part of the year. The echolocation capabilities of different nectarivorous phyllostomids have only been directly compared in one study that exposed four species to a standardized test of wire array avoidance in a flight room (Howell 1974b). This study found that the seasonally insectivorous *A. geoffroyi* and *G. soricina* were able to detect and avoid wires as thin as those detected by insectivorous bats. In contrast, *L. yerbabuenae* performed poorly on this test and performance of *Choeronycteris mexicana* was intermediate between the extremes.

Glossophagines use their echolocation to detect distinctive echoes reflected by flowers (von Helversen and von Helversen 1999; Simon et al. 2011). Conspicuous acoustic properties of a bat-pollinated flower were first described for the legume liana *Mucuna holtonii*. Freshly-opened flowers in this species possess a small concave petal directly above the nectar opening and this “acoustic guide” produces high amplitude echoes conspicous to bats flying nearby (von Helversen and von Helversen 1999). Removing these signals from flowers in the field reduced bat visitation from 88 to 21%. Other plants have modified leaves subtending their flowers with echo-reflecting properties that effectively make them acoustic beacons. Such is the case of the woody vine *Marcgravia evenia*, in which disk-shaped leaves displayed on top of the inflorescences exhibit strong and invariant acoustic signatures (Simon et al. 2011). In controlled experiments with *G. soricina*, the removal of these disk-shaped leaves doubled the time it took the bats to find the flowers. In other bat-pollinated plants lacking obvious acoustic beacon structures, the whole flower itself may likely be the unit of attraction. Glossophagine bats utilize the acoustic properties of flowers during foraging and readily integrate this information with input from other sensory systems according to context and background complexity (Muchhala and Serrano 2015). We expect lonchophyllines and opportunistic nectarivorous phyllostomids to similarly rely on acoustic signals, although there is little research to date in these groups.

Pteropodids are mainly nocturnal, do not have ultrasonic laryngeal echolocation, and have large, conspicuous eyes with tapeta lucida that reflects light. Some roost in dark locations such as hollow trees, caves, and mines. In contrast to phyllostomids, pteropodids had been assumed to orient by vision, except for *R. aegyptiacus* which echolocates with tongue clicks (Yovel et al. 2011). The lingual echolocation by *R. aegyptiacus* is sophisticated and well developed even though it was originally considered rudimentary. It remains to be seen if any pteropodid other than *R. aegyptiacus* uses echolocation for foraging.

The role of night vision in foraging by nectarivorous bats remains largely unexplored. Ultraviolet light detection has been demonstrated for *G. soricina* (Winter et al. 2003). Studies of gene function of UV-sensitive opsins across bats suggest ultraviolet vision in other glossophagines (e.g. *Anoura caudifer*, *L. yerbabuenae*) and some pteropodids (e.g. *Cynopterus sphinx*), but it was apparently lost in obligate cave roosters (e.g. *Lonchophylla mordax*; Kries et al. 2018). Ultraviolet light detection might be advantageous for foraging in dim light conditions such as during twilight hours, or while approaching ultraviolet-reflecting flowers with dark vegetation or a night sky in the background (Winter et al. 2003; Fleming et al. 2009).

9.6 Foraging and Movement Ecology

The physiology, feeding habits, and movement ecology of nectarivorous bat are highly interdependent. For example, *L. yerbabuenae* is the main pollinator of several *Agave* species and readily exploit the clumped distribution of these plants in space and time (Howell and Roth 1981). Similarly, the temporally aggregated blooming of various columnar cacti species in the spring and several *Agave* species in autumn along the Pacific coast of Mexico forms a veritable nectar corridor for these bats that matches their seasonal migration patterns (Fleming et al. 1993). These corridors are crucial for the endangered *L. yerbabuenae*.

More recently, Medellín et al. (2018) showed that *L. yerbabuenae* can travel up to 100 km in a single night. They applied fluorescent powder to bats from a large colony of lactating females, and recaptured marked individuals hours later at two sites about 40 and 50 km away. The bats travelled this far to reach large aggregations of the night-blooming and bat-pollinated columnar cacti, *Carnegiea gigantea*. These 100 km round trips represent the greatest foraging distances that have been accurately determined for any nectarivorous bat.

Spatial movement patterns have also been studied for some species of nectarivorous pteropodids. In Africa, *Megaloglossus woermanni* is the only obligate nectarivore bat species. Weber et al. (2009) showed that *M. woermanni* uses forests as daytime roosts and readily forages in agricultural plantations during the nighttime. The study also showed that females in agricultural landscapes have foraging ranges twice the size of those of males. Frequent use of agricultural landscapes is common in pteropodids in areas with abundant fruit crops, which unfortunately puts these bats in conflict with farmers and expose them to hunting (Frick et al. 2019).

Today, the miniaturization of GPS trackers and acoustic recorders is accelerating the study of movement patterns and foraging behavior. Using these new methods, Egert-Berg et al. (2018) found that *L. yerbabuenae* and *R. aegyptiacus* do not forage in groups, although they do interact with conspecifics in their feeding grounds. This result suggests that nectarivorous bats do not need to forage collectively to find resources that are relatively predictable in space and time, such as flower nectar and pollen. The rapid improvements in bat tracking technologies will surely open many more windows into the movement ecology of nectarivorous bats.

9.7 Nectarivorous Bat Conservation and Pollination Services to Crops

Many studies documenting the economic importance and ecological value of bat pollination have been presented at NASBR. One inspiring conservation success story involves bat pollination of agaves. The glossophagines *L. nivalis*, *L. yerbabuenae*, and *C. mexicana* are the main pollinators of *Agave tequilana* and many other commercially important agave species from which tequila, mezcal, and pulque are obtained (Howell and Roth 1981; Sánchez and Medellín 2007). Rapid expansion of agave cultivation, combined with farming practices that prevented the plants from flowering before harvest, deprived vast agricultural landscapes of food resources for the bats (Trejo-Salazar et al. 2016). This contributed to the low population densities and endangered status that the Mexican populations of these bats have had for many decades (Sánchez and Medellín 2007). Joint efforts by bat biologists, tequila farmers, and conservationists established a program called "bat-friendly tequila", where farmers allow 5% of agave stems per hectare (~222 inflorescences) to flower during the six-month plant reproductive season. Models predicted that this would allow 89 bats to meet their nightly food requirements (Trejo-Salazar et al. 2016). "Bat-friendly tequila" is the first conservation program of its kind and has been highly successful.

In the Old World, there are similar tight relationships between nectarivorous pteropodids and socioeconomically important plants (Fujita and Tuttle 1991). Well-known examples include the Southeast Asian fruit crops of durian (*Durio zibethinus*; Malvaceae) and the legumes *Parkia speciosa* and *P. timoriana* (Fabaceae). These crops are pollinated by multiple pteropodid species, but especially by the specialist nectarivore *E. spelaea* (Stewart and Dudash 2017). Other bat-pollinated plant species in the Old World have multiple uses. For example, the leaves of *Oroxylum indicum* are cooked and eaten, the bark, roots, seeds and leaves are used in traditional medicine, and its fruits and bark are the source of a valuable black dye for coloring baskets (Fujita and Tuttle 1991). Another multiuse species is the bat-pollinated African shea butter tree (*Butyrospermum parkii*), whose seeds provide oil used for cooking, soap-making, and cosmetics (Fujita and Tuttle 1991). A final example are the mangrove species in the genus *Sonneratia* (Sonneratiaceae), which are pollinated by *Macroglossus* and *Eonycteris* bats (Stewart and Dudash 2017). *Sonneratia* species are structurally dominant in mangrove forests across Southeast Asia, providing an important source of timber and charcoal, and help to buffer coastal regions against the effects of severe tropical storms (Fujita and Tuttle 1991; Stewart and Dudash 2017).

Despite the substantial conservation value of pollination services provided by nectarivorous bats, these animals still face many threats. Throughout the world, populations are threatened by habitat loss and fragmentation, pesticide use, direct persecution as pests or for bushmeat hunting, predation by nonnative predators (e.g. brown tree snake preying on *Pteropus mariannus* in Guam), and lack of awareness among the general public (Frick et al. 2019). However, as exemplified by the "bat-friendly tequila" program, these threats can be mitigated through conservation and education efforts that foster interactions among local stakeholders, scientists, and decision-makers.

9.8 Conclusions and Future Directions

In the last 50 years we have learned much about the many fascinating aspects of nectarivorous bat biology. Specialized nectarivore bats are exquisitely adapted to their dietary lifestyle and display an impressive array of physiological, sensory, and behavioral adaptations to exploit floral resources. They quickly process nectar and pollen to obtain energy to sustain their high metabolism, find flowers in the dark using scent, vision, and acoustic cues, and pollinate hundreds of plant species. Several other generalist nectarivorous species also contribute to pollination services, further demonstrating the complex and intricate nature of bat-plant interactions.

There are, however, still many exciting research avenues and knowledge gaps that need to be addressed. For example, the importance of bat pollinators relative to other floral visitors has been poorly explored, yet it is crucial to understand how plant species first evolved to become adapted to bats from ancestors relying on other groups of pollinators. These comparisons should include visitation rates, but also estimates of the quality and quantity of the pollen transferred by the bats and other pollinators. Bats often carry large amounts of pollen in their fur and it is likely that this pollen represents a large pool of donor plants more genetically diverse compared to that transported by other pollinators such as birds or insects. If so, pollen deposited by bats could lead to higher fruit and seed production or result in more vigorous seed germination and seedling growth.

Taxonomically speaking, the species that have been most studied tend to be the most abundant and widespread, resulting in important information gaps concerning basic natural history and ecology of some recently described Neotropical genera (e.g. *Xeronycteris*, *Hsunycteris*) and many poorly-studied pteropodid taxa (e.g. *Melonycteris*, *Notopteris*, *Lissonycteris*, *Micropteropus*). In terms of geographic coverage, medium and high elevation Neotropical phyllostomids have been less studied than their low elevation counterparts, whereas in the Old World much more research has been done on Southeast Asia and Australo-Pacific nectarivorous species than on those from Africa.

Aspects of physiology, sensory ecology, and spatial ecology offer many exciting new research possibilities with the increasing sophistication of GPS trackers, echolocation recording devices, temperature sensors, and other technology. The role of night vision and UV detection during foraging deserves attention, and efforts are also needed to examine the echolocation capabilities of pteropodids. Spatial patterns of foraging and seasonal migration must also be further explored. Bats readily use spatially aggregated floral resources, but they are also capable of long-distance flight. So to what extent do they trapline scattered food plants versus utilizing local resource-rich patches? Other than *Leptonycteris* and some pteropodids, we still know little about the movement patterns of nectarivores. This information is becoming increasingly urgent to address the effects of habitat fragmentation on bat and plant populations. Another important gap concerns those species that utilize different habitat types seasonally (e.g. along elevational gradients). In this regard, dietary studies are still needed for many species to understand how nectarivorous bats supplement their diets with other resources such as insects and fruit, and the extent to which different species can switch to alternative foods during periods of scarcity. Climate change may affect floral resource availability across many scales, which can jeopardize bat populations and the provisioning of their pollination services.

Finally, much needs to be done for the conservation of this important bat guild. The fascinating stories of bats and their flowers are powerful educational tools that can help raise awareness on the importance of nectarivorous bats specifically, and of all bats more generally. Effective conservation efforts involving local communities, farmers, scientists, and decision-makers can be inspired by these stories, giving bats everywhere a chance to continue servicing our ecosystems and societies. We are confident that NASBR will continue playing a pivotal role in the successful exchange of scientific research and innovative conservation initiatives to address the challenges that bats face in our rapidly changing world.

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Chapter 10
Penguins, Falcons, and Mountain Lions: The Extraordinary Host Diversity of Vampire Bats

Gerald Carter, Bridget Brown, Imran Razik, and Simon Ripperger

Abstract Common vampire bats (*Desmodus rotundus*), white-winged vampire bats (*Diaemus youngi*), and hairy-legged vampire bats (*Diphylla ecaudata*) are the only obligate blood-feeding mammals. Despite being parasites, vampire bats can also be viewed as opportunistic hunters, because they can feed on a surprising diversity of animals. Here, we review the evidence for this host diversity in vampire bats as determined through several methods: precipitin tests, stable isotope analyses, DNA sequencing, camera traps, captive experiments, and field observations. *Diphylla* shows the strongest preference for birds, whereas *Diaemus* prefers birds but will also feed on mammals; *Desmodus*, in contrast, shows a preference for mammals, although is capable of feeding on a surprising variety of vertebrates, including mammals, birds, crocodiles, snakes, and lizards. Future topics of inquiry include understanding how the host preferences of each species vary across geographic regions and how host selection by individual bats might depend on social information.

Keywords Vampire bat · *Desmodus* · *Diaemus* · *Diphylla*

10.1 Introduction

Three species of neotropical phyllostomid bats—the common vampire bat (*Desmodus rotundus*), white-winged vampire bat (*Diaemus youngi*), and hairy-legged vampire bat (*Diphylla ecaudata*)—feed solely on blood after being weaned off milk. Each species is the only extant member of its genus (Fig. 10.1). Most of what is known about vampire bats comes from *Desmodus*, which is far more abundant and consequently much better studied than the two other relatively rare species. Due to their special diet, vampire bats demonstrate several unique

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Fig. 10.1 Portraits of the three vampire bats. Shown *left* to *right* are the common vampire bat (*Desmodus rotundus*), white-winged vampire bat (*Diaemus youngi*), and hairy-legged vampire bat (*Diphylla ecaudata*). Photos by Merlin Tuttle, ©MerlinTuttle.org

adaptations to their systems for ingestion (e.g., anticoagulant compounds in the saliva, Ma et al. 2013), digestion (e.g., a lack of intestinal maltase activity, Schondube et al. 2001), and excretion (e.g., specialized kidneys for rapid urination during feeding, McFarland and Wimsatt 1969). Their diet has also influenced their morphology and locomotion (e.g., abilities to jump and run, Schutt et al. 1997; Riskin and Hermanson 2005), sensory abilities (e.g., heat sensors to find blood near the skin surface, Gracheva et al. 2011), development (e.g., a 7-month gestation period, Delpietro and Russo 2002), social behavior (e.g., reciprocal regurgitated food sharing, Wilkinson 1984), and cognitive traits (e.g., a lack of taste aversion learning, Ratcliffe et al. 2003). The bites of vampire bats can transmit the deadly rabies virus to livestock or people, posing a threat to agricultural development and public health in Central and South America (Johnson et al. 2014; Benavides et al. 2016). Much research has, therefore, focused on what types of hosts vampire bats prefer to target.

In 1970, at the first meeting of what would become the North American Society for Bat Research, Bernardo Villa-Ramirez presented on his use of the precipitin test for identifying the origins of ingested blood in the stomachs of vampire bats. In his sample of 18 *Diphylla ecaudata*, he reported that all fed on birds, whereas in his sample of 79 *Desmodus rotundus*, 58 fed on mammals and eight selected birds. He also noted that 13 of the *Desmodus* had stomachs full of milk, though they appeared to be adults. These early observations foreshadowed much of what we would later learn regarding the diets of vampire bats. We now know that *Desmodus* prefers mammals but will also feed on birds, that *Diphylla* strongly prefers birds, and that *Diaemus* might prefer birds but will also feed on mammals (Greenhall 1988).

The apparent adults that fed on milk in the study by Villa-Ramirez were not fully grown individuals, and this was an easy error to make given the slow development of juvenile vampire bats. *Desmodus* provides milk to its pup for up to 10 months (Delpietro and Russo 2002), which is about 6 months after the pups can fly, and more than three times longer than the nursing period for most other species of bats (Jenness and Studier 1976; Kunz and Robson 1995; Hamilton and Barclay 1998; Chaverri and Kunz 2006). This prolonged period of maternal care can eventually transition into mother-daughter social bonds that last for years and involve food sharing through reciprocal regurgitations of ingested blood (Wilkinson 1984; Carter and Wilkinson 2013; Carter and Wilkinson 2015).

The feeding ecology of vampire bats is not straightforward to classify. They are obligate blood-feeders and nutritionally *specialized parasites*; yet paradoxically, it is also useful to think of them as generalized and *opportunistic hunters*. In particular, many reports and observations show that *Desmodus* can parasitize a surprising diversity of animals. Here, we review the evidence for host diversity in vampire bats as determined through several methods, including precipitin tests, stable isotope analyses, DNA sequencing, camera traps, captive experiments, and field observations. We also discuss some remaining questions about their feeding ecology and what methods might resolve them.

10.2 Evidence of Host Specialization Based on Morphology and Physiology

Several adaptations suggest divergent specialized feeding strategies in each vampire bat species. *Desmodus* has several unique morphological adaptations for walking, running, jumping, and feeding on the ground, whereas *Diaemus* and *Diphylla* are adapted for climbing on branches (Altenbach 1979; Hermanson et al. 1993; Schutt and Altenbach 1997; Schutt et al. 1997; Schutt 1998; Riskin and Hermanson 2005; Riskin et al. 2006). These differences match their preferred stalking behaviors in the wild (Sazima and Uieda 1980; Greenhall 1988). Consider how the three vampire bats typically feed on a chicken (Fig. 10.2): *Desmodus* approaches by walking or hopping along the ground to access the feet, *Diaemus* climbs on the underside of a branch to bite the toes, and *Diphylla* also climbs along branches but most often grasps onto the underside of the bird and bites the bare skin near the cloaca (Greenhall et al. 1971; Sazima and Uieda 1980; Greenhall 1988; Carter 2016; Berrío-Martínez et al. 2019; G. Carter pers. obs.). Based on this unique 'tick-like' feeding behavior and the lack of a prominent cleft on the lower lip and chin, Greenhall (1988) suggested that *Diphylla* might actually suck blood, unlike the other vampire bats. However, a recent video recording shows that *Diphylla* licks blood from a wound in a fashion similar to the other two species (Carter 2016).

There is also evidence for physiological adaptations to different types of blood. For example, the anticoagulant salivary compounds and digestive systems of *Desmodus* and *Diaemus* appear most effective when feeding on mammalian and avian blood, respectively (Cartwright and Hawkey 1969; Coen 2002). When forced to consume their non-preferred diet in captivity, both species retain less dry matter and nutrients (Coen 2002). Captive *Diaemus* is thought to require at least some avian blood or it can become ill and die (Uieda 1993; Schutt et al. 1999; Coen 2002). Similarly, captive *Diphylla* often refuses mammalian blood (but see 'captive observations' below) and may starve to death when presented with only mammalian blood (Uieda 1994).

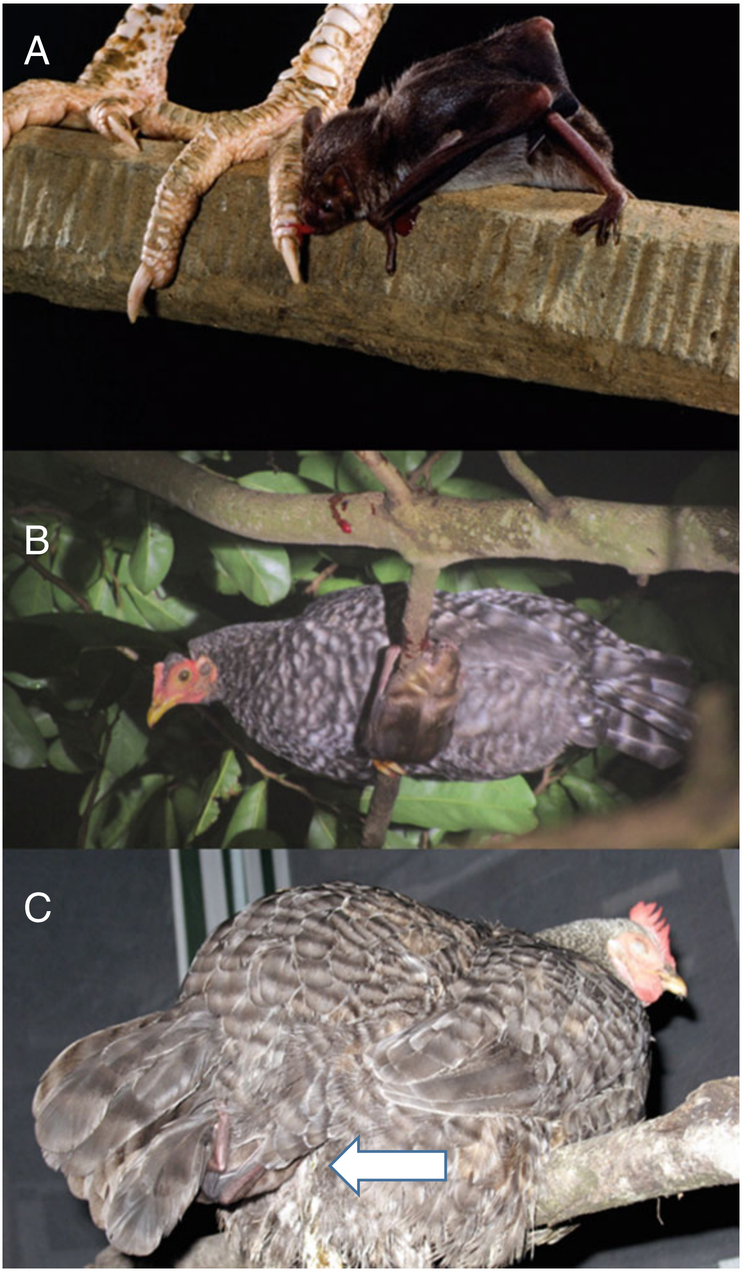

Fig. 10.2 Three different species-typical ways of feeding on a chicken. (**a**) *Desmodus rotundus* feeding on the toes from a walking stance. Photo by Merlin Tuttle, ©MerlinTuttle.org. (**b**) *Diaemus youngi* feeding on the toes of a chicken in a tree in Panama. Photo by Jineth Berrío-Martínez. (**c**) *Diphylla ecaudata* (*arrow*) hanging from the tail feathers and feeding on the skin near the cloaca of a chicken in a flight tent in Mexico. Photo by Gerald Carter

10.3 Precipitin Tests

The precipitin test is used for the identification of blood and was once a routine procedure in forensic science laboratories. The test was later used to infer the hosts of blood-feeding insects, and it was the first method of assessing the diet of vampire bats without direct observation (Greenhall 1970). However, the test is labor intensive and requires collecting serum from all potential host species, as well as the harvesting of antibodies, usually from rabbits, before the analysis. The test can typically identify hosts at the level of the genus or family. Greenhall (1988) tested more than 4000 blood meals in Trinidad and Mexico. In order of the frequency of detection, he found evidence of *Desmodus* feeding on cattle, water buffalo, equids (horses/mules/donkeys), goats, pigs, poultry, sheep, and dogs (Greenhall 1970, 1988). In Costa Rica, the precipitin test confirmed that *Desmodus* ($n = 58$) fed primarily on cattle and horses, and occasionally on goats and pigs (Turner 1975). In Mexico, the test detected that one bat had parasitized a human and another fed on a squirrel (possibly *Sciurus*, Greenhall 1988).

Early observational reports established that *Diaemus* predominantly attacked birds in Trinidad (Goodwin and Greenhall 1961), but more than two decades later, Greenhall (1988) suggested that this species was changing its host preferences to feed increasingly on mammals. Results from precipitin tests showed that *Diaemus* in Trinidad consumed both avian and mammalian blood; 13 of 23 *Diaemus* parasitized mammals, 8 parasitized both mammals and birds, and only 2 exclusively chose the blood of birds. The precipitin test has confirmed that *Diphylla* strongly prefers avian blood (Greenhall 1988). This technique has since been replaced by more efficient and precise methods.

10.4 Stable Isotope Analysis

The isotopic ratio of carbon and nitrogen in consumed foods is reflected in the consumer's tissue (DeNiro and Epstein 1978). Because mammalian livestock primarily consume grass, which fixes carbon via the C4 metabolic pathway, these herbivores have different isotopic signatures of carbon than most native rainforest animals, which derive their nutrients from plants that fix carbon via the C3 pathway (Voigt and Kelm 2006). Stable carbon (^{13}C) isotope signatures can be analyzed within hair, soft tissue, stomach contents, or even fecal samples to assess whether vampire bats prefer to feed on livestock or wildlife. Similarly, stable nitrogen (^{15}N) isotope signatures, including those of individual amino acids ($^{15}N_{AA}$), can help determine dietary components and trophic position (Campbell et al. 2017).

Studies using stable isotopes further verify what the precipitin tests showed previously—*Desmodus* typically feeds on livestock. *Desmodus* in the Peruvian Amazon fed on humans and wildlife in the absence of livestock (Streicker and Allgeier 2016), and groups of coastal-dwelling *Desmodus* fed largely on sea lions

(Catenazzi and Donnelly 2008). Samples from *Diphylla* indicated that it chose hosts at higher trophic levels than *Desmodus* (Campbell et al. 2017), which is consistent with feeding on omnivorous chickens, rather than herbivorous cattle.

The overall picture is that, where livestock are abundant, vampire bats exhibit isotopic signatures that indicate feeding on hosts in the C4 food web, probably cattle and horses. Where livestock are rare, the isotopic signatures reflect both the C3 and C4 food webs—as expected if they were parasitizing both mammalian livestock and chickens or wildlife (Voigt and Kelm 2006; Catenazzi and Donnelly 2008; Streicker and Allgeier 2016; Becker et al. 2018; Ingala et al. 2019). However, even if livestock are locally abundant, some bats within a colony apparently feed repeatedly on native rainforest animals, suggesting that individual bats may use different foraging sites or prefer prey at different trophic levels (Voigt 2009; Streicker and Allgeier 2016). Consistent with such individual variation, the isotopic heterogeneity measured within colonies of *Desmodus* was among the highest observed in any vertebrate population (Streicker and Allgeier 2016).

One advantage of stable isotope analysis is that it can determine longer-term choice of hosts depending on the type of sample. Isotopic ratios can reflect dietary preferences over the past several weeks (wing tissue samples) or 4–6 months (fur samples) (Voigt et al. 2003; Voigt and Kelm 2006). However, the isotopic tests are rather general and do not identify the species of host.

10.5 DNA-Based Techniques

The most precise method for identifying hosts selected by vampire bats is sequencing the DNA of a host obtained from the gut contents or feces of a vampire bat and then matching amplified sequences against reference sequences in a genetic database. The use of fecal DNA even allows completely noninvasive sampling of diet without capturing the bat, but special care must be taken. Amplifying mammalian prey DNA from digested blood can be more difficult than amplifying prey DNA from insect parts in bat feces, due to the prey DNA being highly fragmented, co-amplication of vampire bat DNA, and PCR inhibitors (Bohmann et al. 2018). The first validation of the sequencing approach—identifying chicken DNA from the guano of captive and wild *Diaemus*—also highlighted the need to detect possible contamination using negative controls (Carter et al. 2006). Ongoing advances in sequencing technology have increased the reliability and decreased the time and money required to perform these analyses. Next-generation sequencing and improved extraction protocols have led to high success rates in amplifying and identifying host DNA (e.g., 103/110 blood meal samples yielded host DNA, Bohmann et al. 2018). Although host identification depends on the presence of that host species in the database, these genetic resources are growing, and the method is faster and more powerful than others. DNA-based techniques can also facilitate quantitative analyses, rather than demonstrating mere presence of a specific host in the diet (Bohmann et al. 2018).

Results from DNA-based studies of host selection to date have largely corroborated other methods and provided observations of new wildlife hosts. A study using fecal DNA found that *Desmodus* ($n = 48$), from 18 villages in the Brazilian Amazon, had fed on chickens at a frequency corresponding to their abundance but showed a preference for pigs, whereas dogs and cattle were detected less often than expected based on abundance (Bobrowiec et al. 2015). Four *Diaemus* fed on both chicken and pigs (Bobrowiec et al. 2015).

Bohmann et al. (2018) sampled 110 stomach contents and 8 fecal samples from live vampire bats at 15 sites in the Andes, Amazon, and Pacific regions of Peru. They used the standard mitochondrial genes, 16S rRNA and cytochrome oxidase subunit I (COI) genes, to perform DNA metabarcoding, which amplifies mitochondrial mini-barcodes of taxa within a taxonomic group. As expected, *Desmodus* fed on livestock (cows, pigs, sheep, donkeys, horses, and chickens) but also on tapir (*Tapirus* sp.) at the Amazonian site. All samples from individual bats contained only one taxon suggesting that these bats typically parasitized only one type of host per night. Chickens were underrepresented, compared to their availability, while cows and pigs appeared to be preferred. In contrast, three *Diphylla* fed on chickens but also on two native birds, Spix's guan (*Penelope jacquacu*) and a tinamou (*Tinamus* sp., Bohmann et al. 2018).

Another team analyzed fecal DNA from *Diphylla* and reported evidence for feeding on chickens but also on humans (Ito et al. 2016). However, this result requires additional evidence to be entirely convincing, in our opinion, because the samples identified as human were actually outside the variation of the human reference samples in Genbank, suggesting that other mammals could be the source, and the detection and prevention of contamination is not described in sufficient detail. In most captive studies, *Diphylla* seems unlikely to feed on anything but live birds (see 'observations in captivity below'). However, Ruschi (1951) claimed that wild *Diphylla* fed on pigs, cattle, and horses, although the evidence is not described in detail. Gardner (1977) cites an observation by Ruschi of *Diphylla* feeding on a sleeping human in Brazil. One captive *Diphylla* that was fasted did bite and feed when presented with a human finger (G. Carter, pers. obs.). The question of whether and how often *Diphylla* feeds on mammals (including humans) requires further examination.

10.6 Observations in Captivity

By the end of the 1970s, researchers had placed a surprising variety of animals in captivity with hungry vampire bats to discover what animals they can successfully parasitize (Greenhall 1988; compare Table 10.1). Captive *Diphylla* fed on birds but have often refused to accept the blood of cattle, pigs, or goats or to attack live rats or rabbits (Villa-R 1966; Hoyt and Altenbach 1981; Greenhall 1988; Uieda 1994). Ruschi (1951) observed captive *Diphylla* feeding on birds, including a swallow-tailed kite (*Elanoides forficatus yetapa*).

Table 10.1 Earliest records of each vampire bat species feeding on a specific host

Vampire bat	Host family	Host (family, genus or species)	Host common name	Year	Method	Reference[a]	Common observation[b]
Desmodus rotundus	Bufonidae	*Rhinella marina*	Cane toad	1966	Captive observation	5	
	Boidae	*Boa*	Boa constrictor	1966	Captive observation	5	
	Colubridae	*Elaphe*	Rat snake	1966	Captive observation	5	
		Leptophis	Vine snake	1966	Captive observation	5	
		Pseudelaphe flavirufa	Rat snake	1966	Field observation	5	
	Crocodylidae	*Crocodylus*	Crocodile	1966	Captive observation	5	
	Elapidae	*Micrurus*	Coral snake	1966	Captive observation	5	
	Emydidae	*Pseudemys*	Water turtle	1966	Captive observation	5	
	Iguanidae	*Ctenosaurus*	Ground iguana	1966	Captive observation	5	
	Viperidae	*Crotalus durissus*	Tropical rattlesnake	1966	Captive observation	5	
	Falconidae	*Falco deiroleucus*	Orange-breasted falcon	2011	Camera trap	8	
	Pelicanidae	*Pelecanus*	Pelican	1951	Field observation	5	
	Phalocrocoracidae	Phalacrocoracidae	Cormorant	1951	Field observation	5	
	Phasianidae	*Gallus gallus*	Chicken	1970	Precipitin test	5	X

	Spheniscidae	*Spheniscus humboldti*	Humboldt penguin	1995	Field observation	7	
	Bovidae	*Bos taurus*	Cattle	1933	Field observation	2	X
		Bubalus bubalis	Water buffalo	1961	Field observation	4	
		Capra aegagrus hircus	Goat	1936	Field observation	3	X
		Ovis aries	Sheep	1970	Precipitin test	5	
	Canidae	*Canis lupus familiaris*	Dog	1927	Field observation	1, p. 65	X
	Caviidae	*Cavia porcellus*	Guinea pig	1972	Captive observation	6	
		Hydrochoerus hydrochaeris	Capybara	1980	Field observation	5	
	Cervidae	Cervidae	Deer	1946	Field observation	4	X
		Odocoileus virginianus	White-tailed deer	2011	Camera trap	9	
		Mazama americana	Red brocket deer	2016	Camera trap	11	
		Axis axis	Chital deer	2018	Camera trap	13	
	Cricetidae	*Microtus*	Vole	1972	Captive observation	5	
		Neotoma	“Cave rat”	1972	Captive observation	5	
	Dasypodidae	*Dasypus*	Armadillo	1972	Captive observation	5	
	Echimyidae	*Proechimys*	Spiny rat	1940	Field observation	4	

(continued)

Table 10.1 (continued)

Vampire bat	Host family	Host (family, genus or species)	Host common name	Year	Method	Reference[a]	Common observation[b]
	Equidae	*Equus ferus caballus*	Horse	1526	Field observation	1, p. 13	X
		Equus africanus asinus	Donkey	1970	Precipitin test	5	X
		Equus mulus	Mule	1970	Precipitin test	5	X
	Erethizontidae	*Coendou*	Prehensile-tailed porcupine	1972	Captive observation	5	
	Felidae	*Puma concolor*	Puma	2016	Camera trap	12	
	Hominidae	*Homo sapiens*	Human	1510	Field observation	1, p. 13	X
	Leporidae	*Sylvilagus*	Cottontail rabbit	1972	Captive observation	5	
	Otariidae	*Otaria flavescens*	Sea lion	1951	Field observation	5	X
	Phyllostomidae	*Artibeus jamaicensis*	Jamaican fruit bat	1972	Captive observation	5	
	Sciuridae	*Sciurus*	Squirrel	1970	Precipitin test	5	
	Suidae	*Sus scrofa d.*	Pig	1970	Precipitin test	5	X
	Tapiridae	*Tapirus terrestris*	Lowland tapir	2015	Camera trap	10	
Diaemus youngi	Columbidae	Columbidae	Dove	1969	Captive observation	5	
		Columba livia domestica	Pigeon	1961	Field observation	14	
	Fringillidae	Fringillidae	True finch	1969	Captive observation	5	
	Furnariidae	Dendrocolaptinae	Woodcreeper	1969	Captive observation	5	

	Icteridae	Icteridae	Icterid passerine bird	1969	Captive observation	5	
	Mimidae	Mimidae	Mockingbird	1969	Captive observation	5	
	Numididae	*Numida*	Guinea fowl	1980	Field observation	16	
	Phasianidae	*Gallus gallus*	Chicken	1961	Field observation	14	X
		Meleagris gallopavo	Turkey	1980	Field observation	16	
	Picidae	Picidae	Woodpecker	1969	Captive observation	5	
	Pipridae	Pipridae	Manakin	1969	Captive observation	5	
	Psittacidae	Psittacidae	Parrot	1969	Captive observation	5	
	Thraupidae	Thraupidae	Tanager	1969	Captive observation	5	
	Turdidae	Turdidae	Thrush	1969	Captive observation	5	
	Tyrannidae	Tyrannidae	Tyrant flycatcher	1969	Captive observation	5	
	Bovidae	*Bos taurus*	Cattle	1970	Precipitin test	15	
		Capra aegagrus hircus	Goat	1961	Field observation	14	X
	Caviidae	*Cavia porcellus*	Guinea pig	1961	Captive observation	14	
	Suidae	*Sus scrofa d.*	Pig	1970	Precipitin test	15	
Diphylla ecaudata	Accipitridae	*Elanoides forficatus yetapa*	Swallow-tailed kite	1951	Field observation	17	

(continued)

Table 10.1 (continued)

Vampire bat	Host family	Host (family, genus or species)	Host common name	Year	Method	Reference[a]	Common observation[b]
	Anatidae	Anatidae	Duck	1951	Field observation	17	
		Anatidae	Goose	1951	Field observation	17	
	Cracidae	*Penelope jacquacu*	Spix's guan	2018	DNA sequencing	18	
	Hominidae	*Homo sapiens*	Human	1953	Field observation	17	
	Numididae	*Numida*	Guinea fowl	1951	Field observation	17	
	Phasianidae	*Gallus gallus*	Chicken	1939	Field observation	17	X
		Meleagris gallopavo	Turkey	1951	Field observation	17	
	Tinamidae	*Tinamus*	Tinamou	2018	DNA sequencing	18	

[a] References: 1. Brown (1994); 2. Trapido (1946); 3. Greenhall (1972); 4. Malaga-Alba (1954); 5. Greenhall (1988); 6. Schmidt and Greenhall (1972); 7. Luna-Jorquera and Culik (1995); 8. Muela et al. (2011); 9. Sánchez-Cordero et al. (2011); 10. Castellanos and Banegas (2015); 11. Galetti et al. (2016); 12. Kays (2016); 13. Calfayan et al. (2018); 14. Goodwin and Greenhall (1961); 15. Greenhall (1970); 16. Sazima and Uieda (1980); 17. Moojen (1939); Ruschi (1951) in Gardner (1977); 18. Bobrowiec et al. (2015)

[b] Common observations are those that are corroborated by multiple observations or sources. It is difficult to estimate the frequency of host observations because most references do not provide the number of observations or the sampling effort, but the vast majority of host observations involve these species

Diaemus appears to favor domestic chickens when available but will also feed on mammals (Greenhall 1988). In captivity, they preferred the blood of goats, donkeys, and guinea pigs over that of cattle, but they will feed on cattle blood in captivity and in the wild. When tested for the ability to feed on various wild birds in captivity, *Diaemus* attacked doves, parrots, woodpeckers, woodcreepers, manakins, tyrant flycatchers, mockingbirds, thrushes, orioles, tanagers, and finches, but not a hummingbird, apparently in part because it roosted on a thin branch inaccessible to the vampire bat (Greenhall 1988).

Captive *Desmodus* successfully parasitized an armadillo, porcupine, cave rat, vole, cottontail rabbit, guinea pig, a fruit-eating bat, pelican, crocodile, turtle, marine toad, ground iguana, boa constrictor, coral snake, rat snake, and even a tropical rattlesnake (see Table 10.1 for scientific names, Trapido 1946; Schmidt 1978; Greenhall 1988). Schmidt (1978) reported that *Desmodus* stalks and feeds upon animals the size of guinea pigs or larger, but when presented with mice, the bat instead quickly jumps on the back of the mouse and bites it without necessarily drinking its blood (Schmidt 1978).

Greenhall (1988) highlights the agility of *Desmodus* and its ability to deal with much larger species. He describes a dramatic encounter when a bat was presented with a cave rat (*Neotoma* sp.), which is found in the same caves as the vampire bats. "The rat stoutly defended itself and on one occasion rat and bat engaged in a fist fight, both animals rising on their hindlegs and exchanging blows . . . Joint attack by vampires against one rat presented an uneven fight, and the rat was bitten on its tail, hindleg, nose, and ear, and finally killed" (Greenhall 1988: 118).

Some of his most intriguing accounts describe *Desmodus* facing snakes. In a captive encounter with a slender vine snake (*Leptophi*s), Greenhall (1988: 119) states that "the bat dodged several more strikes until the snake stopped, seemingly tired. The bat bit its back and fled." Even more surprising is his account of a vampire bat's interactions with a snake quite capable of feeding on bats (Greenhall 1988: 119). "A rat snake, *Elaphe* sp., a bat predator often found near caves with *Desmodus*, repeatedly struck at the vampire which skillfully avoided the strikes . . . After some maneuvering, the bat positioned itself facing the snake's head, nose to nose. The vampire bat repeatedly licked the rostral scale until a wound was made and blood flowed . . . The snake remained motionless but flicking its tongue." This atypical 'rasping wound' by licking was described further by Greenhall (1972).

In a similar captive situation, *Desmodus* apparently avoided a ring-tailed cat (*Bassariscus* sp.). For several other species—an opossum, a coyote, a coatimundi, a striped skunk, a tiger cat, and a red-shouldered hawk—*Desmodus* attempted but failed to feed and the bat was itself eaten in each case (Greenhall 1988). Overall, these captive trials demonstrate that *Desmodus* is quite flexible in its ability to feed on many different species, and that *Diaemus* and possibly *Diphylla* can parasitize many birds.

10.7 Field Observations

Most field data on the hosts of vampire bats come from reports of people studying or simply observing a vertebrate animal, and then serendipitously seeing a vampire bat feeding on it. To our knowledge, no one has directly observed the rarer vampire bats, *Diphylla* or *Diaemus*, attacking wildlife in the field. However, *Desmodus* has been observed feeding on capybaras (Carranza 1982), water buffalo (Goodwin and Greenhall 1961), sea lions (Mann 1951; Greenhall 1988; Catenazzi and Donnelly 2008), and sea birds, like pelicans, cormorants (Mann 1951; Greenhall 1988), and penguins (Luna-Jorquera and Culik 1995). One benefit of direct observations is that the observer can describe the natural behavioral interactions between the vampire bat and host. For example, corralling and observing livestock allows description of how the bats approach their target, the part of the body where the bats bite, the reaction of the host, feeding durations, and so on (Greenhall et al. 1971; Crespo et al. 1974; Turner 1975; Wilkinson 1985).

Reported observations of natural feeding behavior in the wild are rare but they are likely to become more abundant with increases in the use of camera traps and public repositories for images and video. Camera traps have shown *Desmodus* feeding on wild feral pigs and collared peccaries (e.g., Galetti et al. 2016; Calfayan et al. 2018; Zortéa et al. 2018), lowland tapirs (e.g., Kays 2016; Gnocchi and Srbek-Araujo 2017; Zortéa et al. 2018), red brocket deer (Calfayan et al. 2018; Zortéa et al. 2018), white-tailed deer (Sánchez-Cordero et al. 2011), chital deer (Calfayan et al. 2018), orange-breasted falcon (Muela et al. 2011), tamandua (Kays 2016), giant armadillo (Zortéa et al. 2018), and even a mountain lion (Fig. 10.3, Leite Pitman in Kays 2016).

Anecdotal reports about the feeding behavior of vampire bats extend back for hundreds of years. Many historical reports of vampire bats describe them feeding on early European conquistadors and their horses (Malaga-Alba 1954; Brown 1994). Some authors have speculated that, prior to the European introduction of cattle to Latin America, vampire bats may have fed on humans in the Maya, Inca, and Aztec populations (Turner 1975). Depictions of vampire bats have often been observed throughout various Mayan ruins (Benson 1987; Brown 1994). *Desmodus* populations have likely benefited from humans more than any other bat species.

10.8 Conclusions and Future Directions

Since Villa-Ramirez's 1970 talk on using the precipitin test to identify the hosts of vampire bats, an expanded toolkit of methods has given much additional insight into the feeding ecology of vampire bats, but many important questions remain. As the diets of vampire bats become easier to study, there is an opportunity to understand regional variations in host preferences both between and within each species. Information on geographic variation in host selection could have important implications for public health and wildlife disease, because the risk of vampire bats

Fig. 10.3 Common vampire bat on a cougar at Los Amigos Biological Station, Peru. Photo by Renata Leite Pitman (originally published in Kays 2016)

transmitting rabies to humans or livestock might increase with changes in the bat's habitat or the removal of preferred hosts (Bohmann et al. 2018). For example, if a population of vampire bats feeds heavily on tapirs and these tapirs are then depleted by hunting, then vampire bats might be more likely to bite humans in nearby villages (Bohmann et al. 2018). Larger populations of *Desmodus* appear to be sustained by stable aggregations of large hosts, such as cattle ranches and breeding colonies of sea lions or sea birds. Breeding aggregations are seasonal, and so prior to the introduction of livestock, vampire bats may have needed to switch hosts throughout the year. Since most studies of the behavior of vampire bats involve populations that depend on livestock, much is still unknown about how these bats cope with the relative scarcity of large hosts in undisturbed habitats. In such situations, vampire bat colonies might be much smaller and the individuals may rely even more on cooperative food-sharing (Wilkinson 1984).

Diaemus and *Diphylla* are both much rarer than *Desmodus*, which might be explained by the ability of *Desmodus* to take advantage of cattle. Cattle are one of the easiest hosts for a vampire bat to feed on because they aggregate in the open, reside in predictable locations, are large and diurnal, and are mostly unable to defend themselves against the vampire bats. Although *Diaemus* and *Diphylla* were long considered avian specialists, it is possible that these preferences vary by region or site (Greenhall 1988). Geographic variation in feeding strategies or nutritional physiology remains to be explored.

The possibility for intraspecific differences in behavioral feeding strategy is also intriguing. For example, individual *Desmodus* are more exploratory at a younger age compared to adults (Carter et al. 2018; Berrío-Martínez et al. 2019), and it is possible that volant juveniles will more often attempt to feed on unfamiliar host species. This hypothesis could be tested by looking at the age distribution of vampire bats that are captured as they approach typical hosts, like cattle, versus atypical hosts, like dogs or other novel animals experimentally introduced to a site. Ages up to 17 years have been recorded in marked wild vampire bats (Delpietro et al. 2017), and ages of unmarked vampire bats can now be estimated from tissue samples using epigenetic clocks (e.g., Wilkinson et al. 2020).

Host preferences might also be influenced by social information. For example, some individual *Desmodus* appear to avoid the risks and difficulty of making a bite by exploiting the bites made by conspecifics (Greenhall et al. 1971; Schmidt 1978; Delpietro et al. 2017). This behavior could result in producer-scrounger dynamics, in which 'producers' that open a wound could be exploited by 'scroungers' that use the same wound or take it over (Barnard and Sibly 1981; Harten et al. 2018). Vampire bats might also learn about possible hosts from other individuals, as seen in the fringe-lipped bat, *Trachops cirrhosus* (Page and Ryan 2006). Given the importance of sociality to vampire bat life, it would not be surprising to find an important, yet undescribed, social component to vampire bat foraging and host preference. With recent advances in technology, such as bat-borne proximity sensors that can assess social foraging (Ripperger et al. 2019a, b, c) such questions will undoubtedly be addressed in the future.

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Part V
Flight

Amy Russell

The 1971 North American Symposium on Bat Research in Albuquerque, New Mexico, included a presentation on randomness in bat homing by Don Wilson and James S. Findley, followed by a discussion of high-altitude flights of Mexican free-tailed bats by Timothy C. Williams et al. Fifty years later, we follow suit with a chapter revisiting homing in bats by Erin Baerwald, Theodore Weller, Dana Green, and Richard Holland, followed by a chapter on bats flying at high altitudes by Gary McCracken, Ya-Fu Lee, Erin Gillam, Winifred Frick, and Jennifer Krauel.

In Chapter 11, Baerwald et al. review 50 years of progress made in our understanding of bat homing behavior. From early studies using displacement experiments and the limited radiotelemetry technologies of the time, Baerwald et al. examine more recent advances in bat homing and navigation. The authors point out limitations of older work in this field, including the assumption that intra-seasonal roost switching did not occur and the use of methodological practices that frequently underestimated home ranges and familiar areas. Examining more recent work, Baerwald et al. discuss the roles of both sensory systems and extrinsic factors guiding orientation and navigation, including magnetic fields, polarized light, olfactory cues, vision, and spatial memory. Notably, recent work by Toledo et al. (2020) adds compelling evidence of detailed cognitive spatial maps in Egyptian fruit bats. Baerwald et al. conclude with a call for further work, pointing out that studies of homing have largely ignored tropical species. Our understanding of homing and navigation in bats globally has important implications for mitigating the effects of wind-energy facilities on bat populations and on predicting the spread of disease and spillover into human populations.

In Chapter 12, McCracken et al. address high-altitude flight in bats. This phenomenon was first documented using radar and was assumed to represent a use of

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high-altitude winds for commuting between roosting and foraging areas. McCracken et al. review more recent dietary, echolocation, and radar studies indicating that bats can forage at high altitudes. Questions remain as to physiological adaptations, behaviors, and sensory cues used for flight and navigation at such extreme heights. The authors conclude by noting special threats that may exist to bats flying at high altitudes, including wind turbines and airplane traffic.

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Chapter 11
There and Back Again: Homing in Bats Revisited

Erin F. Baerwald, Theodore J. Weller, Dana M. Green, and Richard A. Holland

Abstract At the 1971 meeting North American Society for Bat Research (NASBR) in Albuquerque, Don Wilson and James S. Findley presented “Randomness in Bat Homing.” The central tenet of their paper was that homing ability in bats could be explained by chance alone or by some sort of random search [Wilson and Findley (Am Nat 106:418–424, 1972)]. In this retrospective, we assess the knowledge gained from, but also the limitations of, older studies on bat homing and review the advances in our understanding of homing and navigation in bats. Although we have learned much over the last half-century about the orientation and navigational abilities of bats, particularly our understanding of cues and spatial orientation, we still do not know if bats are capable of true navigation nor how they learn to do so. Partly because of technological advances, the study of homing has expanded from bats’ ability to return to roosts after being displaced short distances to determining how bats navigate and find destinations during long-distance seasonal migrations. We advocate for expansion of the study of navigation to include inter-seasonal movements and tropical areas and highlight the need to apply new knowledge of movement and navigation to the conservation of bats.

Erin F. Baerwald and Theodore J. Weller contributed equally to the work

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Homing refers to an animal's ability to return to a known goal (e.g. a nest, roost, or den) after being displaced. The ability to home to familiar sites is both a fascination for the general public and the subject of intense study by scientists aiming to understand the mechanisms that govern it. The study of homing in various taxa, such as birds, insects, sea turtles, and salmonids, made significant advances during the past half-century leading to amazing discoveries about the capabilities of animals to navigate and the cues they use to do so. Despite these findings, an increase in technologies available to study small animals, and an increased interest in the topic of movement ecology, understanding of homing in bats has lagged behind other taxa (Holland 2019). Here we review the study of homing in bats over the last 50 years and argue for its continued importance, not only to understand the specifics of how bats navigate across the landscape, but also for the importance of applying this knowledge to improve conservation outcomes.

Keywords Familiar area · Home range · Homing · Migration · Orientation · Navigation · True navigation

11.1 Homing? What's That?

Before moving forward, some definitions are needed:

1. *Home range* is the area used by an individual for its normal activities, such as roosting and foraging. For bats in temperate areas, it has been applied conventionally to areas used during summer.
2. *Familiar area* is the geographic region an animal uses over the course of a year. For non-migratory animals, familiar areas may be small, consisting of just their home ranges, but for migratory animals, familiar areas may be quite large. In temperate areas, the familiar area consists of summer and winter home ranges and the space used to move between them during spring and autumn migration (Leffler et al. 1979).
3. *Homing*, in the simplest sense, is the ability of an animal to find its way home after being displaced. Displacement can occur within or outside an animal's familiar area.
4. *Orientation* is the ability of an animal to determine the differences between directions and select a specific direction to move toward. It is often referred to as a "compass."
5. *Familiar area navigation* is the ability to return to a specific location from an area where the animal has been before (i.e. from within a familiar area), presumably based on landmarks and/or spatial memory of recognizable features.
6. *True navigation* is the ability to return to a location from an area where the animal has never been before (i.e. from an unfamiliar area) based only on cues detected at the site of displacement. True navigation requires both a "map" (the ability of an animal to determine its position in space relative to its goal) and a "compass" (orientation abilities).

11.2 Starting from Home

At the 1971 meeting of the North American Society for Bat Research (NASBR) in Albuquerque, Don Wilson and James S. Findley presented, and subsequently published, "Randomness in Bat Homing." The central tenets of their paper were that "Investigations to date have been unable to demonstrate whether the mechanism of bat homing is: (1) some innate homing mechanism or navigational abilities such as many species must possess for migration; or (2) randomness, that is, returning to a familiar area by chance alone or by some sort of random search" (Wilson and Findley 1972: 418–419). They concluded that the most parsimonious explanation for homing ability in bats is randomness. If bats are taken away from their roosting area, some proportion will find their way back through chance alone, not through any natural navigational ability. If this is the case, returns will decrease with increasing displacement distances and these data could be used to calculate an expected return percentage (Fig. 11.1) and an expected return curve (Fig. 11.2). To test for homing ability, they compared their conceptual model to rates of return to roosts for bats displaced different distances for individuals of two neotropical species, the black myotis (*Myotis nigricans*) and greater spear-nosed bat (*Phyllostomus hastatus*).

Interest in homing in bats was at its peak in the early days of NASBR. Since then, we have accumulated additional evidence demonstrating the homing abilities of bats, such as fidelity of individual bats to their summer activity areas and specific roost sites (e.g. Lewis 1995). However, research into bats' ability to return to familiar areas and how they do it has slowed in recent decades (Table 11.1). We contend this is due partly to changes in both terminology and technology. Fifty years ago, radio-telemetry was in its infancy. Williams and Williams (1967) used 7-g transmitters to study homing in greater spear-nosed bats. But most researchers of the time did not have access to radio transmitters or study species capable of carrying such large payloads. As a result, displacement experiments were used to understand the radius of animal's home range that, by default, was assumed to be circular and centered on the roost. In the decades since the first NASBR, decreases in the size and cost of transmitters have resulted in more studies aimed at characterizing home range size and habitat composition. Concomitantly there has been a shift, at least in terminology, from homing studies to home-range studies. Emphasis has shifted to understanding sensory systems (e.g. vision) and extrinsic factors (e.g. magnetic fields) that guide orientation and navigation. As a result, we are not much farther ahead on

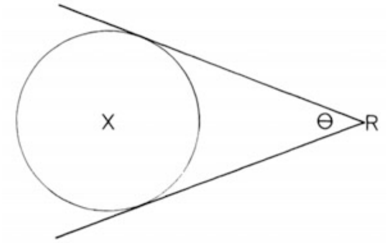

Fig. 11.1 The probability of a bat returning to familiar area (x) when released at *R* is Ø/360. From Wilson and Findley (1972)

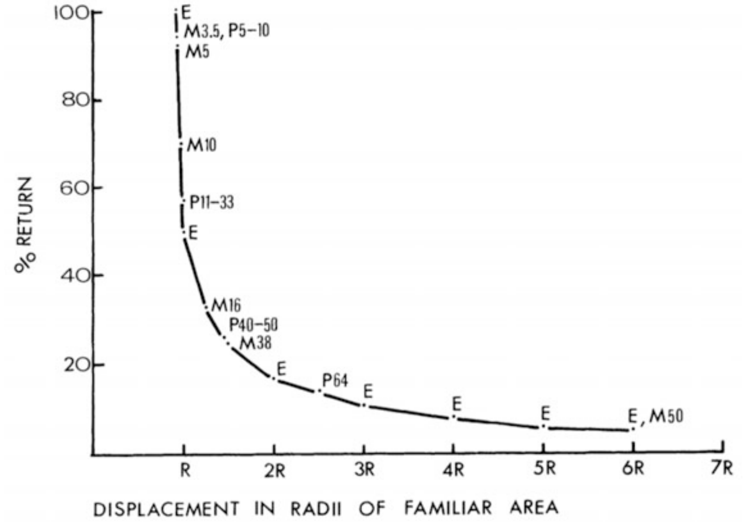

Fig. 11.2 Expected returns of bats displaced various multiples of familiar area radius. E = expected; M = *Myotis nigrans*; P = *Phyllostomus hastatus*. Numbers following M and P are actual distances (in kilometers) for various releases. From Wilson and Findley (1972)

Table 11.1 The number of citations, by decade (as of February 2020), from the Web of Science, within the categories of biology, ecology, or zoology when combining the search term "bats" with "homing" or "orientation" in a topic search. Papers that combined both topics are tallied in both categories

	1960–1969	1970–1979	1980–1989	1990–1999	2000–2009	2010–2019
Homing	8	6	3	0	3	4
Orientation	3	2	3	3	11	24

understanding the extent of bats' homing abilities than Wilson and Findley were in 1972. Why? Is it that navigation research flourished in other taxa (Mouritsen 2018) and bat researchers assumed that if all these other taxa exhibit true navigation, bats must be able to navigate as well?

We have learned a great deal about the complex orientation and navigational abilities of bats in the 50 years since Wilson and Findley (1972) posited that homing in bats occurs by random chance, but we *still* have not demonstrated the limits of homing ability in bats or if bats are capable of "true navigation." Based on what we know from other taxa, particularly migratory birds, it would be remarkable if bats did not show similar abilities to correct for displacements outside their familiar area or to exhibit "true navigation" but, even using modern techniques, this has not been demonstrated conclusively. Nevertheless, given the divergent evolutionary pathways that may have led to migration and navigation in bats versus birds, it is important to continue to evaluate bats in a comparative context.

We contend that much of the early work to understand homing abilities in bats remains unfinished, limiting our ability to understand fully the movement capabilities of bats and the mechanisms used to complete these movements. Although Wilson and Findley (1972) concluded that displaced bats returned to their roost via random searching, it was less than a decade later when Leffler et al. (1979:201) stated, "Bats obviously can navigate successfully within their familiar area, perhaps by use of memorized landmarks." Since then, there have been numerous examples of the sophisticated spatial memory bats possess, but there has been little work describing the details, cues, or mechanisms of how bats learn and remember specific sites or landmarks within their familiar areas. Further, we emphasize that the familiar areas of bats are not simply where they roost and forage during pup-rearing or hibernation seasons. Familiar areas include not only summering and wintering areas but critically important migration routes and mating grounds.

11.3 Limitations of Previous Homing Studies

With no other way to determine home range size of bats, the first researchers investigated homing by capturing bats at their roost, moving them some distance away, releasing them, and then determining whether they returned (Davis 1966). The rationale for these early studies was that the proportion of bats that returned during a displacement experiment was correlated with the homing ability, and thus home range size, of the species. With the benefit of hindsight and modern technologies, we can now appreciate the limitations of this approach for determining the homing ability of bats.

First, and likely foremost, in most cases bats were not displaced far enough outside their home ranges or familiar areas to establish homing distances reliably. They could have found their way back using landmarks and spatial memory or random searching, as Wilson and Findley (1972) suggested. In most cases, bats were displaced <50 km from their roost, but researchers of the time had no way to know nightly foraging distances or distances traveled during seasonal migration. For example, Leffler et al. (1979) displaced little brown bats (*Myotis lucifugus*) up to 161 km, but we now know this species can move up to 464 km from one summer roost to another (Norquay et al. 2013). Long-tailed bats (*Chalinolobis tuberculatus*) in New Zealand were displaced a maximum distance of 20 km (Guilbert et al. 2007) and homed to their roost within 3 days. However, long-tailed bats can travel over 35 km throughout a night (O'Donnell 2001). In general, home ranges and familiar areas of bats are much larger than initially thought, as we are discovering with new technology. For example, Egyptian fruit bats, while having a confined foraging area around a home cave, appear capable of recognizing large landmarks when transported over 100 km away, suggesting an overall larger familiar area compared to their foraging area (Tsoar et al. 2011).

Our ability to determine homing ability or true navigation is also confounded by how frequently and readily bats switch roosts. The concept of intra-seasonal roost switching was virtually non-existent 50 years ago, but it is now well known that many species of bats, particularly those roosting in trees and rock crevices, but also in buildings, switch roosts regularly (Lewis 1995). However, most displacement studies did not conduct intensive repeat surveys of the roost to determine if bats returned eventually. For example, Wason (1978) displaced individuals from four insectivorous species various distances in India, but only surveyed for returns up to 3 days post-displacement. More recent displacement studies that used automated detection of bats with radio-transmitters generally report higher rates of return (Guilbert et al. 2007; Holland et al. 2010). Hence, roost switching and limitations in the ability to detect returning animals may be alternative explanations for what was considered previously to be a failure to home.

11.4 Inter-seasonal Movements

Most experimental work with homing (e.g. displacement studies) has been conducted within the maternity season, and at least in studies involving temperate species, bats were not displaced far relative to their inter-seasonal movements. For example, we know that home ranges change in size depending on season and length of day and reproductive status (Frafjord 2013), possibly confounding homing studies done in a single season (i.e. maternity, migration, or hibernation). We contend that the definition of familiar areas must be expanded to include all areas in which an animal is active, and likely revisits annually, throughout its full annual cycle. Evidence of inter-seasonal movements has been derived largely from recoveries of bats that move between summer and winter roosts in temperate species (Hutterer et al. 2005). But new technologies are allowing insights into the familiar areas experienced by bats at other times of year. Miniature global positioning system (GPS) tags revealed that the autumn familiar area of a male hoary bat (*Lasiurus cinereus*) in northern California included two sites 70 km apart and that it used both in two separate years (TJW, unpublished data). Another hoary bat appeared to wander a minimum of 1000 km during a single month in autumn (Weller et al. 2016). However, the final trajectory of its movement and its ultimate recapture at the original capture site suggest the animal was navigating rather than wandering, perhaps with the aid of a large-scale spatial map. Regardless of how animals are finding their way between seasonal activity areas, the greater distances covered suggests that the cues used by bats during inter-seasonal movements differ from those used to re-locate roosts within a season.

11.5 Cues Used for Orientation and Navigation

To orient and navigate, animals integrate multiple sensory signals over varying scales, likely in a hierarchical fashion. Locating a roost within a home range may rely on vision, echolocation, passive listening, and/or olfaction. At the other end of the spatial spectrum, bats may rely on magnetic field maps and calibration of their compass via solar or celestial cues to make longer distance seasonal movements.

At the largest scale, the earth's magnetic field is the most likely mechanism for orientation and navigation. The magnetic field represents a reliable source of directional and locational information that animals can use as a compass and/or as a map (Wiltschko and Wiltschko 2005). The magnetic vector (i.e. the direction the magnetic field is pointing) can provide directional information and be used to calibrate the compass mechanism. The levels of magnetic intensity and inclination, vary with physical location and can be used to create a map (Fig. 11.3; Wiltschko and Wiltschko 2005).

Studies of other taxa have demonstrated that information gathered from the earth's magnetic field can be combined with additional cues to navigate. For example, both sea turtles and salmon used a combination of chemical and physical cues (e.g. wave and tidal patterns) to guide these animals to and from natal areas while close to shore, but used a magnetic map and compass to navigate at a larger scale in the open ocean (Lohmann and Lohmann 2019). The compass system consists of several interacting signals, but primacy among them appeared to vary depending on the system and study. Similarly, bats use a variety of cues to calibrate directionality relative to the magnetic field (Holland 2019). For example, the greater mouse-eared bat (*Myotis myotis*) used polarized light at sunset (Greif et al. 2014), and soprano pipistrelles (*Pipistrellus pygmaeus*) used the position of the solar disk (Lindecke et al. 2019). One experiment, using pulse re-magnetization (Holland et al. 2008), suggested that bats detect the magnetic field using magnetite in magnetoreceptor cells. In birds, these magnetite-containing magnetoreceptor cells have been implicated in a magnetic map for navigation in unfamiliar areas (Holland and Helm 2013; Munro et al. 1997;). However, Holland et al. (2008) could not distinguish between an effect on a map or a compass or determine where the magnetoreceptor cells were located in bats. The magnetic compass of bats also appears to be polarity based (Wang et al. 2007), unlike the magnetic compass of birds that is based on the angle of magnetic inclination, highlighting differences between these divergent groups.

Although bats perceive and use numerous signals for orientation and navigation at varying scales, research on the sensory systems of bats has focused predominantly on echolocation while detailed information on the use of non-auditory cues and other perceptual abilities of bats is lacking (Holland 2019). For example, olfactory cues are important for navigation in birds (Gagliardo 2013), but this sensory modality remains underexplored in bats, particularly in non-frugivorous species. Although many insectivorous bats are highly specialized for echolocation, it seems unlikely

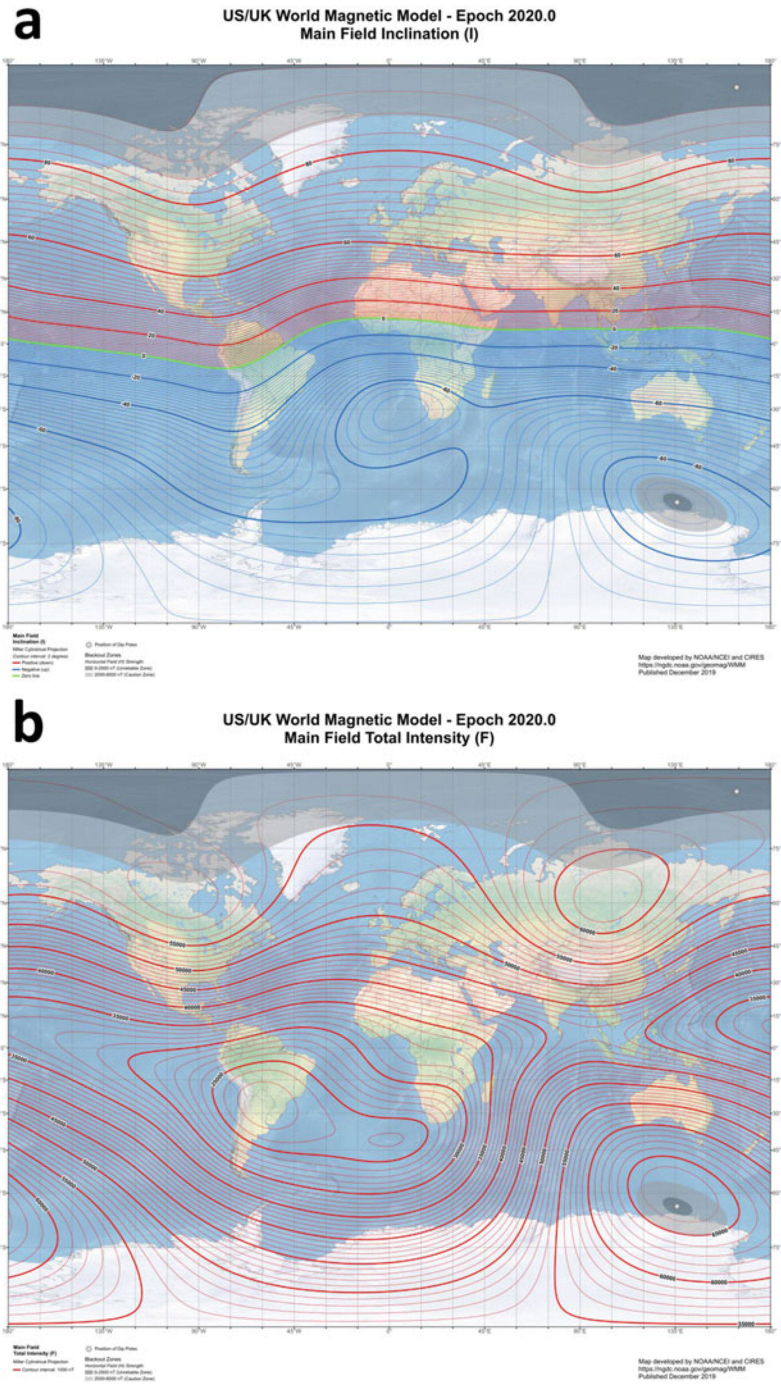

Fig. 11.3 (**a**) The Earth's magnetic field inclination angles are the angles formed between the field lines and the Earth. At the magnetic equator, field lines are parallel to the Earth's surface. The field lines become progressively steeper as one travels north toward the magnetic pole, where the field

that they are using echolocation to navigate from outside their familiar area (Griffin 1970).

There are many reasons to dismiss the use of echolocation for large-scale navigation. Low-frequency sounds travel longer distances than sounds with high frequencies because they are attenuated less by the atmosphere and therefore should be more useful for long-distance navigation. However, the frequencies used by most echolocating species (>10 kHz) have operating ranges of only tens of meters (Griffin 1970; Kick 1982). Besides, echolocation relies on the return of echoes, and if a bat is flying high and away from objects, the animal would not receive echoes in return. Even if bats were using echolocation to navigate, it would need to be used in conjunction with spatial memory and context (i.e. a bat could receive an echo from a tree, but the animal would need to know the specific tree and the position of that tree relative to others) to use it as a navigational aid.

Although we have known for over 50 years that vision is important for homing in bats (e.g. Williams et al. 1966), we are just beginning to understand the specifics of how they use it. Bats are capable of perceiving stars (Childs and Buchler 1981), exploiting post-sunset glow (Buchler and Childs 1982; Holland et al. 2010), and using geographical landmarks and linear structures (Furmankiewicz and Kucharska 2009; Williams et al. 1966) for orientation and navigation. Visual cues apparently take precedence over audio cues and/or echolocation when light is sufficient (Eklöf et al. 2002; Orbach and Fenton 2010). Migratory bats have better visual acuity compared to non-migratory bats (Eklöf et al. 2014), perhaps to see distant features such as stars and post-sunset glow or landscape features in low light. Vision is relied upon heavily for homing in the Egyptian fruit bat (*Rousettus aegyptiacus*; Tsoar et al. 2011). However, when removed from the familiar area with no availability of familiar visual signals, Egyptian fruit bats, while initially disoriented, were able to home to their familiar area and roost (Tsoar et al. 2011), suggesting reliance on an additional mechanism for navigation or well-developed spatial memory. Additional work to understand the use of vision by bats for navigation is needed.

11.6 Remembering the Way

Bats possess excellent spatial memory, which they use extensively while foraging (Barchi et al. 2013; Carter et al. 2010). Spatial memory may also aid in orientation and navigation during migration (Geva-Sagiv et al. 2015), as in other mammalian migrants, such as mule deer (*Odocoileus hemionus*; Merkle et al. 2019) and blue whales (*Balaenoptera musculus*; Abrahms et al. 2019). Examples of long-distance movements (>100 km) between roosts in different seasons suggest that bats also

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Fig. 11.3 (continued) lines are directed straight down into the Earth and the inclination angle is 90°. (**b**) An isodynamic chart of the Earth's magnetic intensity, which tends to decrease from the poles to the equator. Maps from https://www.ngdc.noaa.gov/geomag/WMM/image.shtml possess spatial memory over large spatial scales (Norquay et al. 2013; Rodrigues and Palmeirim 2007), but we do not know how they develop this memory nor how bats select a route and destination for migratory movements during their first year. It does not appear that migration routes are socially transmitted from mothers to young in either hoary bats or silver-haired bats (*Lasionycteris noctivagans*; Baerwald and Barclay 2016). We need studies that explicitly quantify spatial memory in bats: what features do bats use as landmarks and how do they learn and remember them? Early studies will likely be most productive if completed during a single season, when movement distances are typically limited. Understanding how bats develop and use a mental "map" of their surroundings during a single season will complement studies of the cues and mechanisms used by bats for true navigation. We can then work on combining these information streams to determine how bats might develop and use spatial maps that encompass their full annual cycle.

11.7 Integration of Information During Seasonal Movements

Bats may indeed use random, exploratory movements to a certain degree, as Wilson and Findley (1972) suggested. It could be that an individual uses a combination of innate and extrinsic cues to start moving in a suitable direction, but the path it follows is likely not linear nor precise. If the path leads to an endpoint that meets the bat's needs (e.g. new roost, profitable foraging area, suitable hibernacula), then the individual remembers this route and incorporates it into the animal's decision-making process in future years. By this process, a young bat may develop its first spatial memory for migratory movements. Some individual hoary bats in northern California have exhibited inter-annual fidelity to capture sites during autumn (Weller et al. 2016). This fidelity suggests that bats remember and seek specific destinations during their inter-seasonal movements, perhaps in addition to their ultimate winter destination. Are these sites initially discovered by chance, as Wilson and Findley (1972) suggested for intra-seasonal homing at much smaller spatial scales, or are bats using other behavioural cues to locate these sites in the first place? While birds appear to have an innate ability for orientation and navigation through a magnetic compass (Wiltschko and Gwinner 1974), recent research suggests that migratory bats learn to orient and navigate enroute during the first migration (Lindecke et al. 2019).

Bats are flexible in their use of seasonal movements (Rodrigues and Palmeirim 2007), indicating that inter-seasonal movements are not dictated entirely by innate cues, but instead governed by the incorporation of contemporaneous assessment of environmental conditions. For example, if food remains in one part of its range, an individual may decide to delay migration (Richter and Cumming 2006), or if roost temperatures remain suitable in one area, the risks of long-distance movement may not be worthwhile to justify migration (Rodrigues and Palmeirim 2007). Bats also time migratory movements to coincide with favourable weather conditions (Cryan and Brown 2007). In other words, not only do bats possess a large-scale spatial map but they also integrate temporal and local environmental information into decisions about when and whether to migrate.

11.8 Homing: The Next Generation

After a half-century of research, it is clear that bats have the ability for orientation and navigation, but we do not yet understand the scope of those abilities for true navigation or the scale at which bats can return "home" successfully. We have learned much about the sensory modalities and cues that bats have at their disposal, but this has not paid dividends in terms of empirical understanding of homing distances or paths. How do we get at this? Vanishing bearings from translocations (i.e. the direction toward which animals orient following release at an unknown location) have been used to determine the ability of bats to orient (Lindecke et al. 2019) and the mechanisms by which they do so (Holland et al. 2008). These methods can provide invaluable insights into the "compass" side of "map and compass" navigation, but they may not be informative about bats' ability to return home from an unfamiliar area, which is a crucial assessment of navigation ability (Gagliardo 2013). It seems logical that within a seasonal home range bats would rely on landmarks and spatial memory for homing rather than magnetic fields or celestial cues that are more suited to long-distance movements. However, the details of how bats develop and use their cognitive maps, and at what scale, are almost completely unknown.

Ideally, we could track the full path of a displaced bat to determine its endpoint and efficiency (minimization of travel between displacement and goal). Doing so requires technology such as active nocturnal radio-tracking via aircraft and GPS technology that can generate detailed movement tracks over short periods. Currently, both of these technologies have limitations. For aircraft tracking, we are limited by cost and the availability of pilots trained for nighttime telemetry. Satellite telemetry has been used to study movements of bats in excess of 450 g for durations approaching a full year and with locational accuracy in the hundreds of meters (Breed et al. 2010). GPS with capabilities for download via mobile phone networks offers improved accuracy and shorter intervals between locations but are limited to use on bats with masses >500 g (Oleksy et al. 2019). More recently, miniature GPS technology has been used on smaller bats (>15 g; Weller et al. 2016). Miniature GPS units capture and store dozens of locations and can be attached so as to obtain information over multiple months. The primary drawback to miniature GPS is that tags must be recovered to obtain the data; hence miniature GPS is useful in situations where bats return to roosts accessible to humans or where biologists are willing to expend extraordinary effort to recapture free-flying bats. As these technologies advance, they should be extremely useful for understanding heretofore unknowable movement patterns of bats and for use in precise route tracking in displacement experiments.

Although many of the earliest homing experiments were conducted on tropical species (Williams et al. 1966; Wilson and Findley 1972), work with tropical species has waned in recent decades. Given the wealth of bat diversity in tropical regions, this is a missed opportunity to understand the full range of navigational capabilities and strategies in bats. For example, migration is well known in temperate species, but latitudinal and elevational seasonal movements also occur in tropical species (Arnone et al. 2016), however, such migrations are poorly documented. Seasonal movements of tropical bats and the cues used to guide them are underexplored topics deserving of additional attention in future years.

11.9 So What? Conservation Implications of Bat Movements

We need to understand the extent of the homing and navigational ability of bats more than ever because many of the most pressing conservation issues facing bats are directly related to bat movement. For example, one of the biggest threats to migratory bats is fatalities at wind-energy facilities. Most fatalities worldwide are of bats migrating or dispersing during autumn (Barclay et al. 2017). Fatality rates vary considerably within and among regions, but it is not clear these deaths are correlated with migratory routes used by bats, primarily because we do not know if bats use clearly defined migratory routes. If bats are using clearly defined migration corridors based on predictable features, then these areas could potentially be avoided for wind-energy development.

At least some migratory individuals do not follow clearly defined routes, but rather, seem to "wander" (e.g. hoary bats; Weller et al. 2016 and silver-haired bats; McGuire 2019). These circuitous *movements* complicate the narrative that seasonal migrations are driven simply by the response to innate cues. Instead, "wandering" suggests that these species rely heavily on a map that consists of much more than the starting and endpoints of migration. These movements also suggest that bats may make decisions about travel direction and areas to visit using real-time decisions informed by weather, prey densities, and internal assessment of trade-offs between energetic and reproductive needs versus their need to reach their destination. Seemingly erratic movements increase the complexity of defining migratory routes, even for single species of bats, and highlight the challenge of incorporating migratory routes into conservation measures.

In many parts of the world, fruit bats in the genera *Pteropus* and *Eidolon* are reservoirs of zoonotic diseases and viruses, such as Hendra, Nipah and Ebola, which result in deadly disease when they spillover to humans (Breed et al. 2010). Fruit bats can travel long distances during nightly foraging bouts and seasonal migrations, sometimes crossing international borders in the process. Determination of the likely geographic scale and patterns of movement of bats could be helpful for predicting the transfer of viruses within regions and mobilizing disease response actions to protect human health. Because many of the implicated species are large-bodied, they can be tracked using GPS technologies that will allow us to understand their movements in greater detail than is currently possible with smaller species. For example, precise reconstructions of movement routes will facilitate our understanding of the extent to which these bats use navigational cues from the landscape.

The study of homing in bats began 50 years ago as fundamental research to determine the homing abilities of bats in small local areas. Since then, our focus shifted to understanding the sensory basis of orientation, and our knowledge of this topic has increased greatly. We now understand that homing ability in bats is not achieved by random searching, however, the central question of how bats find home within and between seasons remains a mystery. Due to technological advances, both in the ability to study bats in the wild and to assess their orientation abilities under controlled conditions, we are no longer limited to asking questions about how bats orient or navigate within small areas. Rather, we can ask bigger questions about how bats move among their seasonal home ranges and how they find their way in new and unfamiliar areas. Inter-seasonal migrations expand our appreciation of the scale and complexity of bat movements, as well as increasing the challenges of trying to learn about them.

We emphasize that most knowledge of homing and movement in bats has come from temperate species, despite this group comprising a small proportion of bat diversity worldwide. We encourage comparative approaches for the study of homing and movement between temperate and tropical species to enhance our understanding of the full range of capabilities and strategies used by bats. We note, too, that technological advances (Chapter 14, this volume) have allowed us to expand the spectrum of possibilities of what we can learn about bat movement and homing and expect that careful applications of these technologies in future years will advance our understanding of bats movements at multiple spatial scales. As knowledge increases about the navigational abilities of bats within and among habitats during different times of year, it will be critically important to apply that knowledge to bat conservation efforts.

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Chapter 12
Bats Flying at High Altitudes

Gary F. McCracken, Ya-Fu Lee, Erin H. Gillam, Winifred Frick, and Jennifer Krauel

Abstract At the second North American Symposium on Bat Research the first reported use of radar to study flight behavior in bats confirmed that Mexican free-tailed bats (*Tadarida brasiliensis mexicana*) fly at altitudes over 3000 m above the ground. The reasons for these high-altitude flights were unclear, and it was assumed that the bats flew this high to commute to favorable foraging sites. Large numbers of insects now are known to utilize favorable winds at altitudes of hundreds to thousands of meters aloft to assist their long-distance movements. Dietary analyses and deployment of bat detectors to altitudes up to 1100 m confirm that Mexican free-tailed bats alter their behavior to feed heavily on these insects, many of which are major agricultural pests. Next generation radars confirm the movements and high-altitude intersection of bats and insects. Doppler weather radars continuously monitor and archive information on the emergence and dispersal of bats, providing long-term data on the bats' ecology, behavior, and estimates of population sizes. Bat species regularly fly to high altitudes on all continents where they occur, and many of these bats are confirmed or suspected of feeding on migratory insects. The high-altitude habitat remains poorly known, as are the physiological adaptations, behaviors, and sensory cues that bats use to meet the challenges and opportunities of flying at high altitudes. Advancing technologies should continue to aid future research to

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investigate the high-altitude frontier and make discoveries about the ecology and behavior of bats aloft.

Keywords Radar · Bats · Insects · Flight · Echolocation · Foraging · Aeroecology · Ecosystem services

12.1 Introduction

Millions of birds and billions of insects fly at altitudes of hundreds of meters above the ground, comprising more biomass and a greater diversity of organisms than move upon the surface of the earth (Hu et al. 2016). High-altitude flight in bats has received little attention and, until recently, biologists have known remarkably little about the behavior of bats flying at altitudes higher than a few tens of meters above the ground. Numerous bat species are known to fly at high altitudes, but the reasons for these flights are poorly understood, as are possible impacts of high-flying bats on ecosystems below. Studies of how bats interact with the environments that they encounter at these altitudes are nascent, even as these environments are changing. Here, we review radar studies on the flights of Mexican free-tailed bats (*Tadarida brasiliensis mexicana*) to 3000 m above the ground, and we discuss recent research that explores the behavior, ecological impacts, and possible reasons for high altitude flight of this and other bat species that fly to high altitudes.

Scientists discovered during World War II that radar could detect the movements of birds (Brooks 1945; Lack and Varley 1945), and radar ornithology was a well-established field of research (Gauthreaux Jr. 2006) by the time of the first North American Symposium on Bat Research (NASBR). At the second NASBR in 1971, Timothy Williams and colleagues reported the first use of radar to study flight behaviors of bats. Their presentation, "High Altitude Flights of Mexican free-tailed Bats Detected by Radar" was subsequently published under a slightly different title (Williams et al. 1973). This research was funded by the U.S. Air Force after collisions of Mexican free-tailed bats with high-performance jet trainers (Williams et al. 1974). A second presentation resulting from this same project, "The Bat Hazard to Aircraft: Environmental Impact with a Vengeance" was contributed to the fifth NASBR by Leonard Ireland and colleagues in 1974.

Pioneering radar ornithologists, including Sidney Gauthreaux, Ronald Larkin, and Thomas Alerstam, occasionally detected "bat-like" flight in radar targets (personal communications to D.R. Griffin), but it was largely assumed at the time of the early NASBRs that bats, unlike birds, usually flew close to the ground (Williams et al. 1973). Mexican free-tailed bats were an exception, and as early as the 1920s, observers at cave-roosting sites in the American southwest commented on the high-altitude departures and return flights of these bats (Campbell 1925). In the 1950s, visual triangulation with the aid of binoculars was used to estimate that the bats departing from caves in central Texas ascended to altitudes of at least 3000 m above ground level (AGL) and that groups of bats returned to the caves from similar altitudes in the early morning (Davis et al. 1962). From the stomach contents of bats returning from foraging, Davis et al. (1962) estimated that each Mexican free-tailed bat consumed about 1 g of insects each night, and extrapolation to the great numbers of bats in a large colony suggested the nightly consumption of many tons of insects. Because there were no known populations of insects at 1000 s of meters AGL, it was assumed that the bats went aloft to take advantage of favorable tail winds that assisted the bats' travel to distant foraging grounds where they would find plentiful supplies of insects (Davis et al. 1962).

Williams et al. (1973) confirmed many of the earlier observations of Davis et al. (1962), and also provided new information and raised new questions. We discuss the pioneering radar study of Williams et al. (1973) and briefly review the almost 50 years of subsequent research on the behavior and ecology of bats at altitudes of hundreds to thousands of meters AGL that followed this first study. Members of at least five families of bats are now documented to fly regularly or occasionally at high altitudes (Table 12.1), but not all (e.g., Pteropodidae; Parsons et al. 2009; Tsoar et al. 2011) are feeding aloft. Bats from at least four families (Emballonuridae, Molossidae, Rhinopomatidae, and Vespertilionidae) forage at high altitudes. The bats that are identified or suspected of feeding at high altitudes are similar in morphology, flight dynamics, echolocation patterns, and feeding strategies to those of Mexican free-tailed bats. Notably, they have high wing-loading and high aspect ratio wings that provide for rapid flight in open airspace (Norberg and Rayner 1987), and they frequently forage for insects above vegetational clutter using relatively low-frequency echolocation calls (Denzinger and Schnitzler 2013). Mexican free-tailed bats remain the most extensively studied of high-flying bats, and our review will focus primarily on this species. However, accumulating evidence from across the globe suggests that feeding at high altitudes occurs wherever bats occur (Table 12.1).

12.2 Williams, Williams, and Ireland, 1967–1973

From 1967 to 1971, Williams et al. (1973) used three different types of radar—search, height-finding, and weather—to study bat flights in central Texas while not interfering with the normal operations of Randolph and Lackland Air Force bases and the San Antonio International Airport. Echoes from the radars confirmed that after evening emergence from several caves, large numbers of bats ascended to altitudes of more than 3000 m AGL (Fig. 12.1). The radars also showed echoes in morning hours that were assumed to be groups of bats assembling above caves, before disappearing below the azimuth of the radar's view. In evening hours, radar echoes from expanding groups of emerging bats covered areas as large as 400 km^2, and the echoes from the leading edge of these groups expanded at speeds that ranged from 7 to 105 km/h (mean = 40 ± 25 km/h). The direction of movement differed on different nights, and on some nights, different groups appeared to go in different directions; however, the directions of movement on any given night did not seem to

Table 12.1 Bat species documented to fly at altitudes higher than 100 m above ground level, with type of evidence for high-altitude flight ([1]radar, [2]acoustic recordings, [3]onboard GPS, [4] diet, [5]visual inference, and [6]airplane strike), maximum recorded altitude, documented feeding activities, and the source (s) of report

Taxon	Evidence type	Altitude (m)	Feeding?	Source
Molossidae				
Tadarida brasiliensis	1,2,4,5,6[a]	3000	Yes	Williams et al. (1973); Davis et al. (1962); McCracken et al. (2008)
T. macrotus	2	300	Yes	Griffin and Thompson (1982)
T. spp (Africa)	2	500	Yes	Fenton and Griffin (1997)
T. teniotis	3,4	680	Yes	Mata et al. (2016); O'Mara et al. unpublished data
Chaerephon plicatus	2,4	200+	Yes	Nguyen (2018)
Vespertilionida*e*				
Lasiurus cinereus	6	2500	?	Peurach (2003)
Lasionycteris noctivagans	6	460	?	Peurach et al. (2009)
Nyctalus noctula	3	800	?	O'Mara et al. (2019a, b)
N. lasiopterus	4	500	Yes	Popa-Lisseanu et al. (2007); Ibáñez et al. (2016)
N. aviator	4	?	Yes	Fukui et al. (2013)
Ia io	4	?	Yes	Thabah et al. (2007)
Rhinopomatidae				
Rhinopoma microphyllum	3	600	Yes	Cvikel et al. (2015)
Emballonuridae				
Taphozous theobaldi	3	800	?	Roeleke et al. (2018)
T. mauritianus	2	500	Yes	Fenton and Griffin (1997)
T. melanopogon	5	250	Yes	Siefer and Kriner (1991)
Pteropodidae				
Pteropus policephalus	6	1524	No	Parsons et al. (2009)
Rousettus aegyptiacus	3	122	No	Tsoar et al. (2011)

[a]Mexican free-tailed bats (*Tadarida brasiliensis mexicana*) are the most commonly reported bat involved in airplane strikes. Airplane strikes at unrecorded altitudes include other species from the bat families Molossidae, Vespertilionidae, Emballonuridae, Hipposideridae, and Pteropodidae (Peurach et al. 2009)

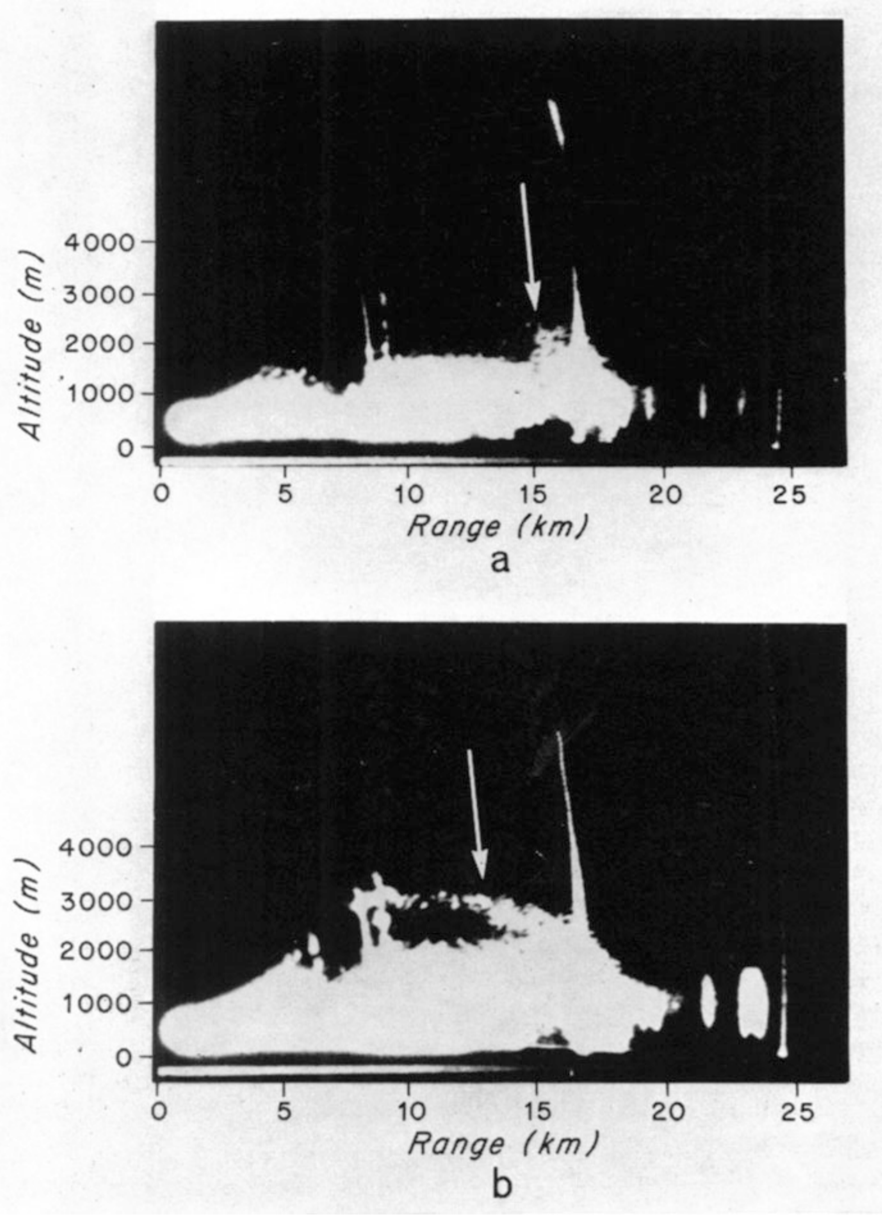

Fig. 12.1 Altitudinal distribution of bats emerging from Bracken Cave. (**a**) Taken at 2110 hours Central Daylight Savings Time (CDST) showing the pattern of ground echoes in the area. The bats are seen as the small mound rising toward the tip of the white arrow. Vertical lines are range marks in the Range Height Indicator display. (**b**) Taken at 2125 hours CDST illustrating the development of a layer of bats (white arrow) leaving the cave. Altitude in meters above sea level is at left; ground level in this area is at about 300 m. Range (distance) of target from the radar is at the bottom of each figure (from Williams et al. 1973)

result from the bats drifting with prevailing winds. All in all, the radars confirmed "rapid, well-directed, high altitude flight" (Williams et al. 1973: 807). The strength of the echoes diminished as the bats dispersed, so nothing more could be inferred about where the bats were going.

Observations from a helicopter confirmed that the bats were the source of radar echoes above Bracken Cave (Williams et al. 1973). The helicopter flew to a maximum altitude of 1500 m, where observers saw bats in the helicopter's floodlights, with the greatest numbers of bats occurring at about 500–800 m AGL. Observers in the helicopter did not see insects at the higher altitudes, but insects were abundant below 200 m. Above 200 m, groups of bats flashed through the floodlights of the helicopter in rapid, horizontal flight. The erratic, darting flight that is associated with feeding was not observed above 200 m, whereas many of the bats below 200 m were obviously feeding. Williams et al. (1973) concluded that the bats above 200 m were not foraging, and the authors suspected that the bats were going to these altitudes to find favorable winds for traveling to more distant foraging areas. However, with the data and technology available, they could neither confirm nor refute any hypotheses as to why the bats flew so high.

12.3 Diet and Insect Migrations

Although Davis et al. (1962) estimated that an individual bat consumed about 1 g of insects each night, detailed energetic studies (Kunz et al. 1995) demonstrated that during periods of peak energy demands a lactating female Mexican free-tailed bat could consume over 70% of her body mass, or about 8.6 g of insects, each night. This nightly rate of consumption, when extrapolated to the 100 million reproductive female Mexican free-tailed bats that were estimated to inhabit the caves of central Texas (Davis et al. 1962), suggested that these bat populations might harvest almost 1000 tons of insect biomass every night (McCracken and Westbrook 2002). The question of where the bats were locating such a large number of insects thus became an even larger issue than envisioned by Davis et al. (1962).

We now know that billions of insects comprising thousands of tons of biomass are constantly moving in the boundary layer of the Earth's lower atmosphere at altitudes of hundreds to a few thousands of meters AGL (Hu et al. 2016). These high-altitude insect movements occur on all continents except Antarctica, and frequently involve insects that are major agricultural pests (Drake and Farrow 1995). For example, the Winter Garden Region in south-central Texas is an important agricultural area, and field studies since the 1980s have employed radar and meteorological methods to track the movements of billions of noctuid moth pests, in favorable winds at high altitudes, from source populations in Mexico into south-central Texas (Wolf et al. 1990; Westbrook et al. 1995; Westbrook 2008).

The possibility that migratory insects provide a food resource to Mexican free-tailed bats was first suggested by an analysis of insect fragments in the bats' diet that revealed striking variation in what the bats ate during the course of a single night

(Whitaker et al. 1996). Over a 5-day period in June, bats feeding before midnight ate mostly beetles (Coleoptera) whereas those feeding before dawn ate mostly moths (Lepidoptera), at a time of year when moth migrants from areas to the south would be expected to increase in abundance in early morning (Whitaker et al. 1996). Lee and McCracken (2005) tested the hypothesis that this variation in the bats' diet was linked to the noctuid moth migrations by examining insect fragments in the feces of bats over three summers from May to August, from three different caves in Texas. Daily and seasonal patterns of insect consumption were similar at the three sites and closely correlated to the patterns of emergence, migration, and availability of noctuid moths that had been previously documented in the region (Wolf et al. 1990; Westbrook et al. 1995). In follow-up studies, the use of ground-level pheromone traps to quantify the abundance of migratory insects was coupled with fecal DNA assays to determine the incidence of migratory insects in the bats' diet (McCracken et al. 2012; Krauel et al. 2018a). Between May and October, the incidence of corn earworm moths (CEW; *Helicoverpa zea*) in the bats' diet closely matched seasonal fluctuations in CEW moth abundance that was measured at nearby field sites (McCracken et al. 2012). A 3-year study investigating diets of Mexican free-tailed bats further documented that the incidence of migratory insects in the bat diet was related to weather-driven insect migratory events (Krauel et al. 2015), and that bats consumed at least 21 species of migratory insects and 44 species of agricultural pests (Krauel et al. 2018a). These results supported the accumulating evidence that migratory insects were an important food to Mexican free-tailed bats, and that the bats provided valuable ecosystem services by limiting crop damage and reducing the need for pesticides (Cleveland et al. 2006; Federico et al. 2008; Lopez-Hoffman et al. 2014; Maine and Boyles 2015). However, these dietary studies did not address whether bats were feeding on insects at high altitudes.

12.4 Bats Feeding at High Altitudes

By the time of the first NASBR, the ability of researchers to eavesdrop on the perceptual world of bats using ultrasonic detectors was advancing rapidly. However, because ultrasonic signals attenuate rapidly, they are detected, at best, over a few tens of meters from the signaler (Griffin 1971). Thus, activity by bats at higher altitudes above the ground was inaccessible to ground-based acoustic technology. In the 1980s, Donald Griffin and colleagues conducted field studies in North America, Australia, and Africa that circumvented the atmospheric attenuation of acoustic signals by placing acoustic detectors coupled with transmitters (radio microphones) on helium-filled blimps and kite-balloons at altitudes at which bats were suspected of foraging (Griffin and Thompson 1982; Fenton and Griffin 1997).

In the southwestern United States and in North Queensland, Australia, ultrasonic calls were recorded from 100 to 300 m AGL, and in both continents the bat activity at these altitudes was sometimes greater than the activity observed near ground level (Griffin and Thompson 1982). In North America, the echolocation calls of the bats aloft were identified as originating from Mexican free-tailed bats and from a related species, the big free-tailed bat (*Nyctinomops macrotis*). In Australia the sounds were attributed to two different species of *Tadarida*. At all locations, detection of feeding buzzes suggested that bats were foraging at these altitudes. In Africa, researchers documented at least four different species of bats at altitudes as high as 600 m AGL, with evidence that the bats were feeding as high as 500 m AGL (Fenton and Griffin 1997). The species aloft in Africa could not be positively identified to species, but six of the seven possible species were attributed to the family Molossidae that includes *Tadarida*; the seventh species feeding at up to 500 m in Africa was tentatively identified as an emballonurid, the Mauritian tomb bat (*Taphozous mauritianus*). A related species from the Emballonuridae, either the black-bearded tomb bat (*Taphozous melanopogon*) or the naked-backed tomb bat (*T. nudiventris*), also had been observed feeding at about 250 m AGL in India (Siefer and Kriner 1991).

During a week-long field campaign in July 1986, Donald Griffin, Sidney Gauthreaux, and Gary McCracken observed bats and insects in central Texas, using the radio microphones described by Griffin and Thompson (1982) and a portable radar and height-finding system developed for studies of bird migration (Gauthreaux 1984). Using this same system, Gauthreaux had observed targets up to 800 m AGL in South Carolina that darted about erratically, suggestive of foraging bats and suspected to be Mexican free-tailed bats. In Texas, the radar system showed numerous small insect-like targets and larger targets with flight behaviors characteristic of foraging bats. The radio microphones recorded many bat echolocation calls including feeding buzzes that were recorded to 200 m AGL. However, the researchers failed in their goal of aligning the systems to allow simultaneous viewing and recording of the same targets (Griffin et al., unpubl. data).

12.5 Bats Feeding at High Altitudes on Migratory Insects

The migratory movements of billions of noctuid moths in the prevailing winds of the atmospheric boundary layer were investigated using free-floating tetrahedral balloons that were released near the sites of insect emergences in the Lower Rio Grande Valley and ballasted to float with the insects at 500–1000 m AGL into central Texas and beyond (Westbrook et al. 1995). Radio microphones attached to these balloons transmitted the echolocation calls of Mexican free-tailed bats at altitudes ranging from 490 to 930 m AGL, with feeding buzzes recorded up to 750 m AGL, confirming that the bats were feeding within the flows of migrating insects (McCracken and Westbrook 2002; McCracken et al. 2008). Attachment of multiple radio microphones to the tether lines of kites (McCracken et al. 2008) further confirmed that Mexican free-tailed bats were flying to at least 1200 m AGL, which was the maximum altitude reached by the recording system, with feeding buzzes recorded as high as 860 m AGL. Peak recorded bat activity occurred at 400–600 m AGL, which was consistent with the altitude of peak density of migrating insects within the atmospheric boundary layer (McCracken et al. 2008;

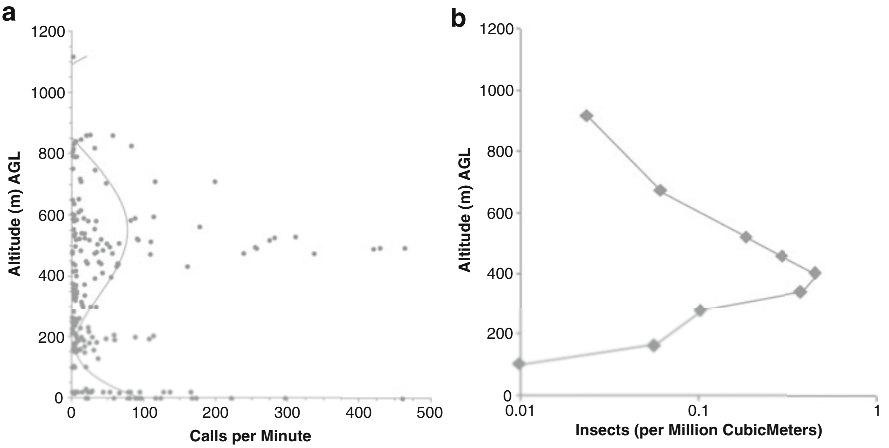

Fig. 12.2 (**a**) Altitude versus echolocation calls per minute recorded by radio microphones suspended from kites. Data show a significant fourth-order polynomial fit of calls per minute versus recording altitude ($R^2 = 0.13, P < 0.0001, Y = 94.80 - 1.219x + 0.00523x^2 - 7.36E^{-6}x^3 + 3.22E^{-9}x^4$), with the highest levels of bat activity at ground level and at 400–600 m AGL. While altitude is the independent variable for this regression, it is shown on the Y-axis for comparison to (**b**). (**b**) Altitude versus noctuid moth densities as estimated from X-band radar. Peaks of bat activity and moth density correspond at the altitude that is typical for the low-level wind jet in central Texas (from McCracken et al. 2008)

Westbrook 2008; Fig. 12.2). Furthermore, Krauel et al. (2018b) showed that foraging activity by Mexican free-tailed bats at high altitudes increased on nights when migratory moths were more abundant during the autumn migrations of insects. The altitudinal convergence of bats and moths supported the hypothesis that the bats exploit the resource of migratory insect populations.

12.6 NEXRAD Doppler Radar

The US Weather Service established a network of Doppler radar (WSR-88 NEXRAD) facilities in Texas in 1995, providing researchers with a tool that could continuously and simultaneously view both bats and insects (Horn and Kunz 2008; Westbrook 2008; Fig. 12.3). Doppler radar images of Mexican free-tailed bats emerging and dispersing from multiple roost sites continued to support many findings of the first radar studies that documented rapid, well-directed, high altitude flight by bats (Williams et al. 1973). These included similar estimates of the speed of dispersal, documentation of flight directions varying night to night, and flights that were not in the directions of prevailing winds (Horn and Kunz 2008).

Because of the diminution of radar echoes with distance from the targets, the radar provided little information on the behavior of bats as they dispersed at greater

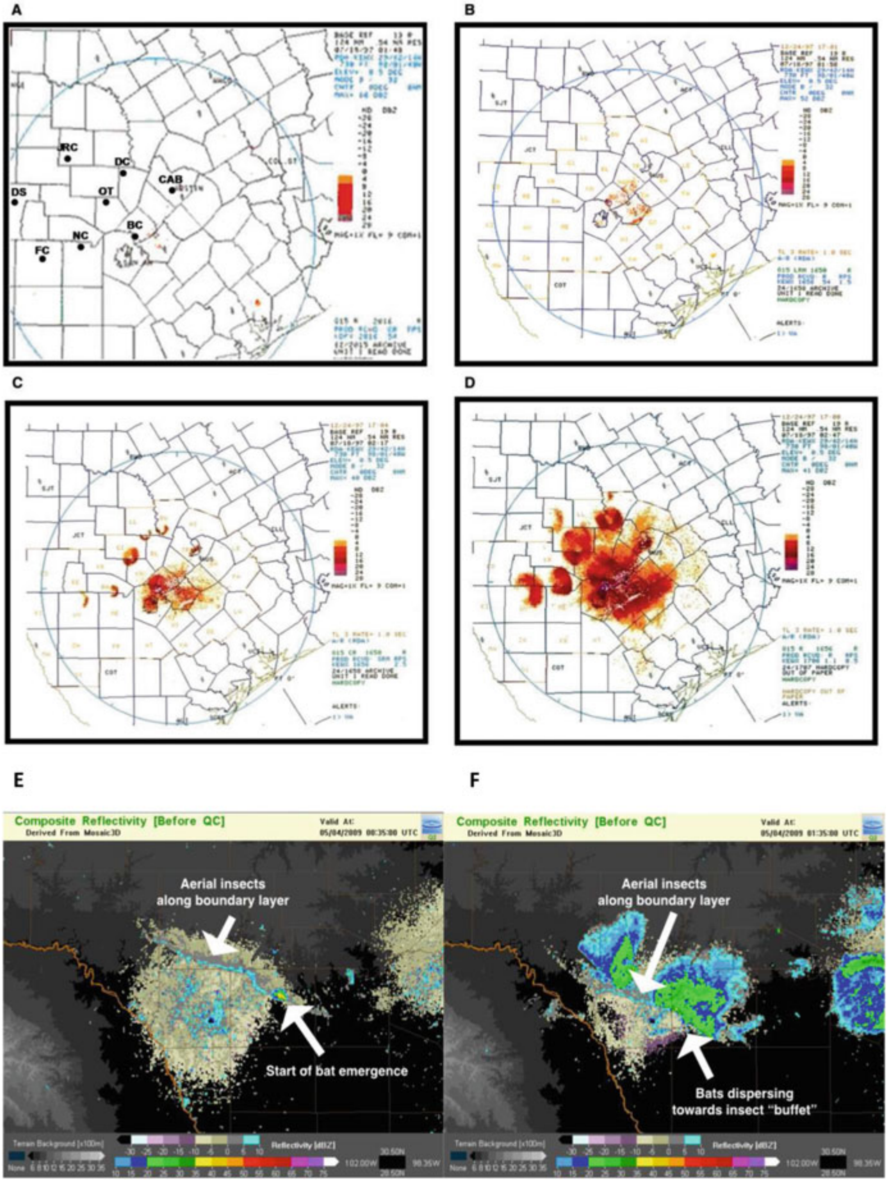

Fig. 12.3 Reflectivity images from NEXRAD WSR-88D Doppler radar at New Braunfels, Texas ((**a**) through (**d**)) and NEXRAD mosaic composite doppler images ((**e**) and (**f**)). (**a**) Clear weather image showing the locations of major roost sites on the night of 18 July 1997, just prior to bat emergence, (**b**) 15 min, (**c**) 30 min, and (**d**) 45 min after the onset of the bats' emergence. *DS* Devil's sinkhole, *FC* Frio cave, *NC* Ney cave, *JRC* James River cave, *OT* old tunnel, *DC* Davis cave, *BC* Bracken cave, *CAB* Congress Avenue bridge (from McCracken et al. 2008). ((**e**) and (**f**)) NEXRAD mosaic composite images of the same area on the night 5 May 2009, showing emerging bats and a band of aerial insects pushed by a cold front, (**e**) at the onset of the bat emergence, and (**f**) emerging bats (s) dispersing towards layers of aerial insects (from Frick et al. 2017)

distances from roosts and became less dense in the aerosphere (Horn and Kunz 2008). However, the continuous monitoring and archiving of the high-altitude flights of bats by Doppler radar over seasons and years provided an incredible resource to address many ecological and behavioral questions. These included examining the long-term effects of weather and changes in climate on the emergence and dispersal behaviors of the bats (Frick et al. 2012) and confirming and expanding earlier ground-based studies indicating that the bats emerge earlier and stay out longer in conditions of drought (Lee and McCracken 2001). Other work documented shifts in migration patterns of the bats that were consistent with expectations of climate change, including earlier arrival at maternity colonies in spring and the occurrence of newly established overwintering colonies in Texas (Stepanian and Wainwright 2018). Doppler reflectivity also provided the ability to estimate colony sizes remotely and to document changes in colony sizes through time and at different roost sites (Chilson et al. 2012b).

12.7 Echolocation and Behavior Aloft

The echolocation calls of bats that forage in open airspace are designed to detect prey over large distances in an environment where echoes from background objects should not affect prey detection (Denzinger and Schnitzler 2013). Bats belonging to this guild of open-airspace aerial foragers utilize low-frequency narrowband calls with long durations, and these bats are mainly members of the same four families (Emballonuridae, Molossidae, Rhinopomatidae, and Vespertilionidae) that are known to feed at high altitudes (Denzinger and Schnitzler 2013). In addition, the echolocation and foraging behaviors of high-flying bats appear to respond to changes in atmospheric conditions as altitudes increase and prey become more widely dispersed (Fig. 12.4).

Attenuation, or reduced signal strength with distance, is a function of call frequency as well as air pressure, temperature, and humidity (Snell-Rood 2012). Attenuation increases with decreasing air pressure, increasing temperature, and to a lesser extent increasing humidity. Bats respond to altitude-related attenuation by lowering call frequency (Griffin 1971). However, the extent to which Mexican free-tailed bats lowered their frequency with altitude was greater than expected solely for attenuation compensation (Gillam et al. 2009).

One explanation for the use of lower-than-expected frequencies at high altitudes is that animals are responding to more widely dispersed prey at higher altitudes. Emitting calls that are more narrowband, lower in frequency, and longer in duration would increase the detection distance of insect prey (Griffin and Thompson 1982). Further, a narrower bandwidth concentrates neural activity in the auditory system, also improving detection range (Schnitzler and Kalko 2001). Mexican free-tailed bats have a highly flexible echolocation call structure (Gillam and McCracken 2007) and shift call parameters with altitude (Gillam et al. 2009). In the presence of migratory moths at high altitudes these bats extend the duration of calls, which

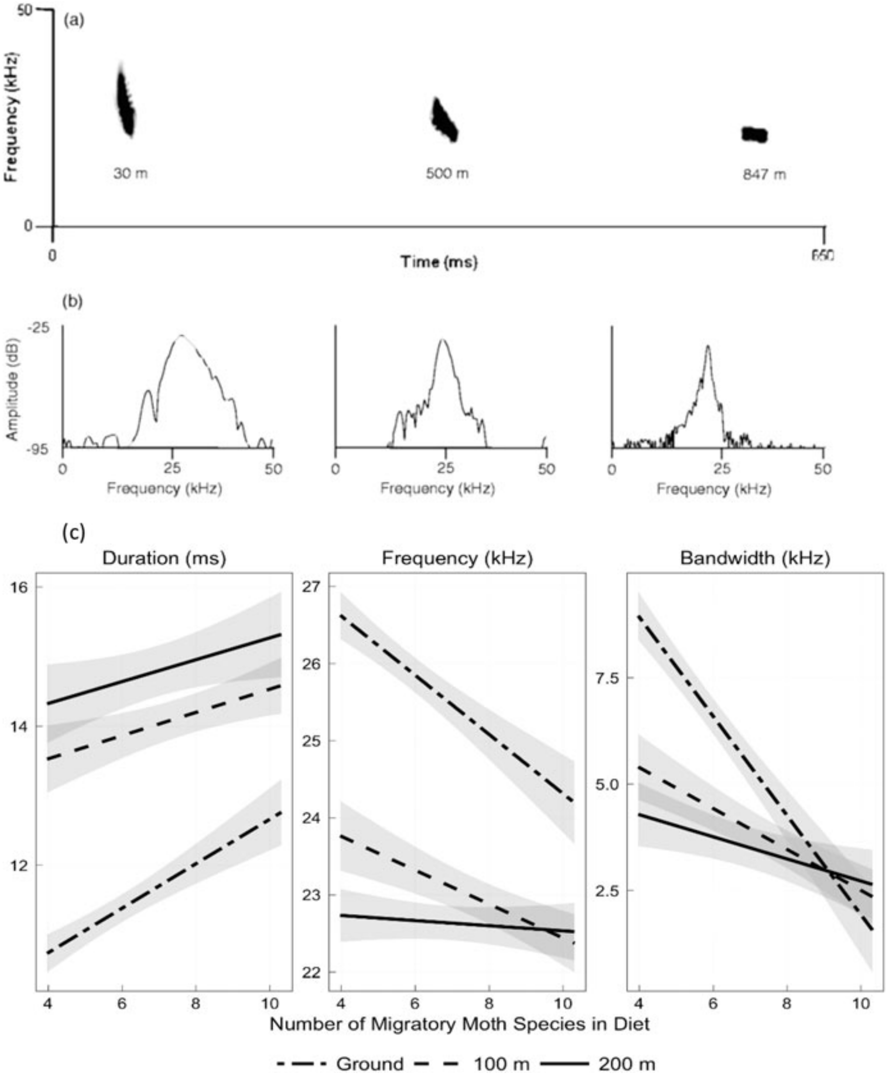

Fig. 12.4 Changes in echolocation call parameters of Mexican free-tailed bats with altitude and the availability of migratory moths. (**a**) Spectrograms of calls recorded at 847, 500 and 30 m AGL. Calls were recorded from radio microphones suspended from kite balloons. Spectrogram was computed using a 512-point fast Fourier transform (93.75% overlap). (**b**) Energy spectrums for calls depicted in A. Each spectrum corresponds to the call depicted directly above, in the spectrogram. These signals do not reflect the absolute structure of all calls recorded at a particular altitude but are presented to illustrate the altitudinal variation in signal structure (from Gillam et al. 2009). (**c**) Observed changes in (1) call duration (ms), (2) frequency of maximum energy (kHz), and (3) bandwidth (kHz) in search phase calls at ground level and at approximately 100 m and 200 m AGL. Lines represent change in call parameter values at each altitude with increasing moth diversity. Shaded areas indicate 95% confidence intervals on linear regression. The horizontal axis represents the number of migratory moth species found in bat diet on the night the call was recorded. Call duration increased, and frequency and bandwidth decreased at higher altitudes; a similar effect was found, especially at ground level, as moth diversity increased (from Krauel et al. 2018b)

would increase their likelihood of detecting glints from distant prey (Krauel et al. 2018b; Fig. 12.4).

While these adaptations to echolocation calls should increase the chances of finding widely dispersed prey at high altitudes, they also come with limitations. Fine prey discrimination generally involves broad-bandwidth calls (Schnitzler and Kalko 2001) and use of long, narrowband, low-frequency calls likely reduces detection of small prey items. However, this call parameter profile could function as a mechanism for selecting larger prey in any environment. Evidence suggests that during moth migration events, Mexican free-tailed bats adjust call parameters to target larger moth prey preferentially, even at ground level (Krauel et al. 2018b).

Bats also may use other behavioral approaches to find highly dispersed prey at high altitudes. Social foraging, particularly eavesdropping on foraging calls of other bats, could be a method of extending the effective distance of echolocation searching. Gillam and McCracken (2007) used echolocation playbacks to free-flying Mexican free-tailed bats at ground level to demonstrate that animals were most strongly attracted to call sequences that contained terminal buzzes, which are indicative of feeding. Data from echolocation recording devices that are small enough to be carried by a bat showed that *Rhinopoma microphyllum* foraged within eavesdropping range at least 41% of the time during periods characterized by highly patchy prey sources (Cvikel et al. 2015).

12.8 Future Directions: Ecology, Orientation, Physiology, and Conservation

Little is known about the aeroecology of bats at high altitudes. Conditions such as wind speed and direction, temperature, humidity, and air pressure vary at different altitudes but not necessarily in smooth gradients (Bonner and Paegle 1970). Temperature and humidity may increase with altitude, especially at night (Drake and Farrow 1988). Turbulence generated by differences between air masses creates boundary layers, which can function to define habitat patches (Wood et al. 2006). For example, migratory insects occur in layers at altitudes with favorable wind speeds, directions, and temperatures, and appear to find and remain in these habitats by sensing micro-turbulence (Drake and Farrow 1988; Chapman et al. 2011). Imagery from mosaics of NEXRAD radar data suggests that Mexican free-tailed bats in Texas will forage on concentrations or "buffet lines" of insects along boundary layers (Frick et al. 2017; Fig. 12.3e, f). However, the extent to which bats perceive and navigate this structure to take advantage of aerial prey habitats is unknown. The integration of data from insect- and bat-sensing radars, data from GPS and echolocation recorders that can be carried by bats, aerial microphone arrays that can map bat movements, and fine scale recording of meteorological data should provide broad-scale and fine-grained information on bat movements aloft and bat-insect interactions.

Bats have anatomical and physiological adaptations that allow for efficient oxygen uptake and transport such as very large hearts and large lungs with a very thin alveolar-capillary barrier (Canals et al. 2011), and Mexican free-tailed bats have exceptionally high hematocrits (Black and Wiederhielm 1976). While these are clearly responses to the energetic demands of flight, whether some bats have physiological adaptations for high-altitude flights remains unclear. Physiological stress from reduced temperatures or reduced availability of oxygen (Voigt et al. 2018) may be overemphasized, as bats in pursuit of insects at several hundred meters aloft are still flying at over 90% of partial pressures of O_2 at sea-level, and in air temperatures that can exceed surface temperatures by as much as 10 °C (Drake and Farrow 1988). Williams et al. (1973) questioned whether bats have physiological adaptations for high-altitude flights, and that question remains unanswered.

Williams et al. (1973) also speculated that olfaction and audition would be inadequate for orientation at thousands of meters AGL and suggested that high-altitude flights may be guided using stars or large visual landmarks. Recent evidence suggests that Egyptian fruit bats (*Rousettus aegyptiacus*), which find their food on the ground, fly to altitudes above 100 m AGL for viewing distant landmarks and navigating long distances (Tsoar et al. 2011). Some insect-eating bats also are known to detect and orient to magnetic cues (Holland et al. 2006) and to use sunset and light polarization patterns, presumably obtained by vision, to calibrate a magnetic compass (Holland et al. 2010; Greif et al. 2014) that would allow navigation. Many bats undoubtedly employ these (and probably other) sensory mechanisms when migrating at high altitudes. GPS tags attached to bats now make it possible to track the daily movements and activity of migratory bats (Weller et al. 2016), and in noctules (*Nyctalus noctula*), we have the first documentation of high-altitude migratory flights in bats (O'Mara et al. 2019a). We expect many future studies using emerging technologies to document the long-distance, high-altitude movements of bats and the navigational cues that guide these movements (Voigt et al. 2017).

Lastly, the numerous threats to high-flying bats in the Anthropocene, including wind-power development, need better assessment and evaluation (Voigt et al. 2018). Although not discussed by Williams et al. (1973), recommendations from their work significantly reduced the risks to Mexican free-tailed bats from impacts with aircraft (Williams et al. 1974). To this day, airplane traffic at Randolph and Lackland Air Force bases and the San Antonio International Airport is regulated using advanced generations of radar technology and real-time monitoring of bat flights. For high-flying species, such as Mexican free-tailed bats that are reliably detected with Doppler radar, use of radar networks to monitor populations and track spatial and temporal movement patterns can assist conservation efforts by identifying areas with high densities of aerial bats and providing information on when bats are aloft and potentially at risk for collisions with wind turbines or aircraft (Chilson et al. 2012a). Evidence of dramatic decreases in insect abundance, the so-called 'insect apocalypse' (Wagner 2020), suggests that reductions in the availability of aerial insect prey poses yet another concern for high-flying bats.

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Part VI
Heterothermy

Allen Kurta

Bats are extraordinary creatures, with many intriguing traits, including the smallest adults and largest neonates of all mammals and flight speeds greater than those of any other vertebrate. Many bats also have the ability to use torpor, lowering their body temperature in a controlled manner, for hours or days at a time, before raising it back to normothermic levels. Research on different aspects of heterothermy have been the focus of presentations at the North American Symposium on Bat Research since its inception, although most early studies only involved animals held in captivity and acclimated to laboratory conditions. Beginning with the pioneering work of Eugene Studier and Brian McNab in the 1970s and Thomas Kunz and Paul Racey in the 1980s, chiropteran biologists have shifted their focus from simple measurements of body temperature and oxygen consumption in the laboratory to more-integrative approaches that use data from captive and wild animals, exploring the linkages among ecology, behavior, body temperature, metabolic rate, and other aspects of physiology.

The following two chapters deal with somewhat different aspects of heterothermy, but both emphasize the transition from simple to multi-factorial perspectives over the last five decades. The first chapter by Johnson et al. focuses on hibernation and examines how views have changed concerning the features that signify a suitable hibernaculum, as biologists slowly realized that torpor has costs as well as advantages. Throughout the chapter, the authors use three competing hypotheses to explore winter habitat selection and nicely demonstrate how knowledge of the physiology of hibernation is pertinent to the management and conservation of bats, especially in light of the epidemic of white-nose syndrome in North American species.

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In the second chapter, Dzal et al. borrow from the field of ethology and innovatively frame their discussion of heterothermy in temperate-zone bats in terms of the four complementary areas of inquiry (mechanism, ontogeny, phylogeny, and adaptive significance) that were delineated by Niko Tinbergen in 1963. The authors rightfully point out that the fourth area of inquiry is the most challenging to a thorough understanding of heterothermy, mainly because of the difficulty in quantifying survival and fitness for bats in general. Dzal et al. conclude their chapter by showing the value of applying an integrative, Tinbergen-like approach to the subject of white-nose syndrome.

Chapter 13
The Winter Worries of Bats: Past and Present Perspectives on Winter Habitat and Management of Cave Hibernating Bats

Joseph S. Johnson, Anna S. Blomberg, Justin G. Boyles, and
Thomas M. Lilley

Abstract Winter is a time of fascinating changes in biology for cave-hibernating bats, but it is also a time of vulnerability. Unsurprisingly, assessments of winter habitat for these mammals and how it can be managed have been a focus of many researchers involved with the North American Society for Bat Research over the last 50 years. Over this time, a paradigm shift has occurred in the way scientists think about factors driving selection of winter habitat, especially temperature. To illustrate this change, we review three hypotheses seeking to explain microclimate selection in cavernicolous bats. The first, which we call the "Colder is Better Hypothesis," posits that bats should select cold microclimates that minimize energy expenditure. The "Hibernation Optimization Hypothesis" suggests that bats should select microclimates that reduce expression of torpor to balance energy conservation against non-energetic costs of hibernation. Finally, the "Thrifty Female Hypothesis" asserts that females should select colder microclimates than males to conserve energy for reproduction. We discuss these hypotheses and the shift from viewing hibernation as a phenomenon driven solely by the need to conserve energy in the context of hibernacula management in North America. We focus on both historical and recent conservation threats, most notably alteration of thermal regimes and the disease

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white-nose syndrome. We urge against returning to an over-simplified view of winter habitat selection in response to our current conservation challenges.

Keywords Conservation · Ecophysiology · Hibernation optimization · Physiology · Torpor · White-nose syndrome

13.1 The Winter Worries of Cave-Hibernating Bats

To the uninitiated, hibernation may appear as an uneventful process consisting of weeks of inactivity in a dark, unchanging environment. However, decades of research have taught us that hibernation is far more interesting. Although the life of a hibernating bat occurs at a much different pace than during summer, the winter lives of bats are dynamic, and the study of winter ecology is both rich in literature and riddled with gaps in knowledge. During winter, bats are not only under selective pressure to conserve energy, but face several competing physiological and ecological demands that must be balanced along with opportunities such as mating (Thomas et al. 1979, 1990; Humphries et al. 2003). Bats respond to these pressures in diverse ways, including periodic arousals, behavioral changes, and habitat selection (Boyles et al. 2007, 2008; Jonasson and Willis 2012). Although we have learned much about the winter lives of bats in the last 50 years, cavernicolous species are currently more imperiled than ever, and proper conservation and management of these animals will require detailed mechanistic understanding of habitat selection during hibernation.

The first report on hibernation presented at the North American Symposium on Bat Research (NASBR) was “Status, Winter Habitat, and Management of the Endangered Indiana Bat, *Myotis sodalis*,” by Stephen Humphrey in 1975. Although not the first study on the winter worries of bats (Hock 1951; Twente 1955; McNab 1974), this presentation and its subsequent publication (Humphrey 1978) articulated concepts that still remain relevant in bat conservation. Humphrey correlated natural disasters, modification of cave entrances, and disturbance by humans to population declines and temperature changes inside hibernacula. Importantly, he also predicted that if winter disturbance from humans were eliminated and temperature regimes restored to 4–8 °C, populations of Indiana bats would recover. At that time, a narrow range of low temperatures was believed to be favorable due to the well-studied effect of temperature on metabolism (Hock 1951; Twente 1955; McManus 1974). Coming soon after passage of the Endangered Species Act of 1973 in the United States, Humphrey’s connection between energetics and decline of a listed species was pivotal, and for decades, belief that suitable winter habitats were those with a narrow range of cold temperatures, conducive to maximum energy savings, was the dominant paradigm (Richter et al. 1993; Tuttle and Kennedy 2002).

Recent studies, though, have shifted our view of hibernation to emphasize that bats must balance more than energy during winter (Thomas and Geiser 1997; Humphries et al. 2003; Boyles et al. 2007). These studies benefited from decades of prior research, as well as technological advances allowing more accurate measurements of the hibernating environment and hibernator physiology. There is now copious evidence against misrepresentation of hibernation as a period when bats require stable, cold temperatures (Boyles et al. 2007; Brack 2007; Kurta and Smith 2014). Unfortunately, this knowledge has not always translated to more effective conservation of bats because we still lack a fundamental, mechanistic understanding of many important aspects of winter ecology. Our goal here is to summarize literature describing our evolving knowledge of selection of winter habitat and implications of these studies for conservation and management. While our review is not exhaustive, it aims to put current knowledge into a theoretical context, especially regarding the role of temperature. We summarize factors known to contribute to microclimate selection, both within and among species, and across environments. We then examine attempted management approaches and the need to adapt to the current challenges of white-nose syndrome (WNS) in North America.

13.2 Factors Driving Microclimate Selection in Winter

To illustrate how interpretation of winter habitat selection has evolved over the last several decades, we describe three hypotheses representing previous and contemporary views focused on temperature. The earliest hypothesis explaining microclimate selection by hibernating bats, which we call the Colder is Better Hypothesis, posits that bats select hibernacula with ambient temperatures (T_a) that minimize their torpid metabolic rate (TMR), thus minimizing energy spent over the entire hibernating season (Fig. 13.1a). This hypothesis assumes that overwinter survival is negatively correlated with energy spent during hibernation and that this selective pressure alone drives use of winter habitat. TMR decreases with T_a down to a threshold (T_{min}), below which hibernators must increase TMR to avoid freezing. Energy savings are maximized at T_as $>$ T_{min} because internal microclimates vary during winter, and periodic drops in T_a below T_{min} cause hibernators to incur greater energetic costs than hibernating at T_as consistently above T_{min} (Buck and Barnes 2000; Boyles and McKechnie 2010). Hibernation at cold T_as also saves energy because torpor bouts are longer at lower temperatures (McNab 1974; Brack and Twente 1985; Dunbar and Tomasi 2006). Given that energetic cost of arousals dominates the energy budget of a hibernating bat, increasing duration of torpor bouts can significantly reduce energy demand over the entire winter (Thomas et al. 1990; Jonasson and Willis 2012).

Numerous biologists during the twentieth century reported bats hibernating at cold T_as, seemingly in support of the Colder is Better Hypothesis (McManus 1974; Nagel and Nagel 1991; Tuttle and Kennedy 2002). Nevertheless, such studies frequently also reported variation in T_as selected, and eventually, variation within and among most species became apparent (Webb et al. 1996). Also at odds with Colder is Better were examples of cold hibernacula with absent or declining bat populations (Gore et al. 2012), warmer sites where populations were not decreasing (Tuttle and Kennedy 2002), and results of studies from latitudes farther north

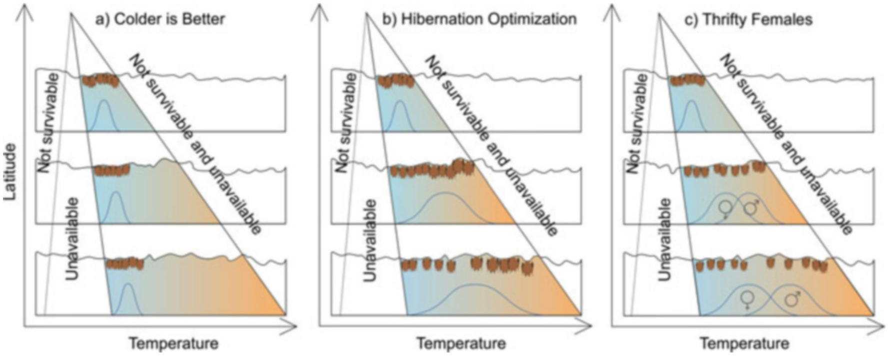

Fig. 13.1 Conceptual diagrams of hypotheses predicting winter microclimate selection in cavernicolous bats. Each panel shows the hypothesized distribution of bats across a thermal gradient within a single hibernaculum (x-axis), which is expected to vary latitudinally (y-axis). The Colder is Better Hypothesis (**a**) posits that bats should select cold microclimates to maximize energy savings. The Hibernation Optimization Hypothesis (**b**) posits that bats should select microclimates that allow for survival while also reducing torpor expression. The Thrifty Female Hypothesis (**c**) asserts that females should select colder microclimates than males because female fitness is influenced not only by winter survival, but also by the need to emerge from hibernation with sufficient fat stores for reproduction

(Fenton 1970; Kurta and Smith 2014). An explanation for some of these observations began to emerge by the turn of the century, with realization that maintaining higher rates of metabolism during hibernation may be beneficial for non-energetic reasons (Humphries et al. 2003). Costs of torpor are not fully understood but include reduced immune function, exposure to predation and abiotic events, loss of physiological advantages of euthermy, and disruptions of homeostatically controlled processes such as sleep (Humphries et al. 2003; Heller and Ruby 2004; Bouma et al. 2010). Thus, successful hibernators balance competing costs and benefits of torpor, and this revelation led to the articulation of new hypotheses predicting winter habitat selection (Boyles et al., In Press).

The Hibernation Optimization Hypothesis posits that bats should select habitats where microclimates allow for survival while reducing use of torpor (Boyles et al. 2007). This hypothesis predicts that bats should select cold T_as when energy is scarce but also predicts bats should avoid cold T_as when possible to minimize costs of torpor (Fig. 13.1b). Implicit to this hypothesis is the expectation that individuals vary in habitat selection based on their unique ecology and physiology. Support for this hypothesis has been found among little brown myotis (*M. lucifugus*) with the observation that bats with more body fat, which can afford more frequent arousals than bats with smaller energetic reserves, select warmer T_as (Boyles et al. 2007). Likewise, captive greater mouse-eared bats (*M. myotis*) selected warmer than expected T_as for hibernation and spent more time in torpor when food deprived (Wojciechowski et al. 2007). However, Natterer's bats (*M. nattereri*) with less fat were observed using shorter torpor bouts in England, where foraging on warm evenings is possible (Hope and Jones 2012). The Hibernation Optimization

Hypothesis could be used to make predictions regarding interspecific differences in habitat use. For example, although different species often vary in microclimatic preference, suitable explanations are lacking for why some species prefer warmer or colder T_as (McNab 1974; Raesly and Gates 1987; Brack 2007; Kurta and Smith 2014; Johnson et al. 2016). Comparisons of different species selecting from the same range of available microclimates may reveal important differences in ecology, such as energy needed for reproduction or migration, or in physiology, such as metabolism or heat and water loss.

Within species, there are additional drivers of variation in use of torpor and habitat selection, beyond existing fat reserves. Jonasson and Willis (2011) developed the Thrifty Female Hypothesis based on different patterns in loss of body mass by males versus females during winter. The Thrifty Female Hypothesis suggests females should express torpor to a greater degree during winter because they face greater selective pressure to maximize energy savings than males (Fig. 13.1c). Unlike males, female bats need additional fat reserves to reproduce successfully upon emergence from hibernation (Kunz et al. 1998). Thus, females have less energy available to mitigate costs of torpor than males and are predicted to select colder microclimates than males with the same amount of fat. Since its articulation, the idea that each sex balances costs and benefits differently has been noted in some (Rughetti and Toffoli 2014) but not all species (Hope and Jones 2012). Furthermore, female selection of both relatively warm and cold regions within the same hibernaculum (Boyles et al. 2007), despite pressure to maximize energy reserves, demonstrates females still respond to the need to minimize costs of torpor, at least to some degree.

The latter two hypotheses reflect the importance of having a range of thermal environments accessible during winter, although it is not well documented how available temperatures vary across large geographic areas and whether this variation actually affects hibernators. One study, conducted using the unique temperature gradient present in Florida (McNab 1974), demonstrated the potential impact of research in this area. This study paired measurements of temperatures available in hibernacula with observations of where gray myotis (*M. grisescens*) and tricolored bats (*Perimyotis subflavus*) hibernate. Finding that the larger gray myotis was limited to northern Florida, where colder temperatures were available, McNab (1974) concluded that warmer temperatures in southern Florida posed challenges to obligate hibernators. Smaller tricolored bats can hibernate farther south in Florida than gray myotis, reflecting differences in ecology or physiology between species, although the possibility has not been examined further. Available temperatures vary with latitude on an even larger scale across North America, influencing opportunities for bats to reduce torpor use given their energetic constraints (Fig. 13.1). Latitudinal variation in available temperatures may result in local adaptation and acclimatization in populations of species with large geographic ranges, but few studies have examined this topic (Dunbar and Brigham 2010).

Although temperature is the best-studied aspect of winter habitat, other microclimatic factors including water content of the air, air flow, and barometric pressure can also affect habitat selection (see Perry 2013 for a review of factors determining underground microclimates). Actual water vapor pressure and saturation vapor pressure of hibernacula can be used to determine vapor pressure deficit, an index of evaporative water loss (EWL) in bats and an important factor leading to arousals (Thomas and Geiser 1997; Ben-Hamo et al. 2013; Kurta 2014; Kurta and Smith 2014). Some species are more vulnerable to EWL during winter and select more humid winter habitats as a result (Wermundsen and Siivonen 2010; Kurta and Smith 2014). Among bats with similar rates of EWL, a trade-off may exist when selecting more humid habitats because lower rates of EWL result in increased use of torpor and experiencing its associated costs (Thomas and Geiser 1997; Boyles et al. 2017). However, our understanding of the role of humidity and other microclimatic factors such as air flow or barometric pressure is rudimentary compared to our understanding of temperature effects.

Clearly, research conducted in the nearly 50 years following Humphrey's study has demonstrated hibernation is not driven by a single environmental factor, but rather a collection of factors, with hibernators balancing competing pressures with limited energy. It is, therefore, not surprising that winter habitat selection within well-studied species shows considerable variation. Unfortunately, the need for management recommendations on how to provide, protect, and restore winter habitat is more pressing than ever, and extends to most cavernicolous bat species. Next, we discuss how knowledge of factors influencing winter habitat selection has been used in management in the past, how new data have challenged old assumptions, and how WNS has added an additional dimension to this challenge.

13.3 Management Challenges

When Humphrey presented his work in 1975, the newly minted Endangered Species Act of the United States directed agencies to avoid adversely affecting critical habitat. Humphrey noted that closing caves or obstructing airflow was tantamount to their degradation or destruction, and recommended restoration (Humphrey 1978). While many restorations met with success, not all such efforts have resulted in population responses, suggesting a fundamental disconnect between our understanding of hibernation ecology and population recovery. Given this disconnect and the changing paradigm surrounding habitat selection in winter, there is a need to reconsider practices for the management of hibernacula. Although all possible management actions merit attention, we focus our discussion solely on temperature.

Restoration or improvements of thermal habitats within hibernacula historically has revolved around efforts to reduce T_a at sites in the middle and eastern United States (latitude $\leq 42°$N) (Richter et al. 1993; Tuttle and Kennedy 2002; Johnson et al. 2016). Unintended warming of hibernacula in this region is well known at sites modified with walls and gates, which impede inflow of cold air during winter (Humphrey 1978; Richter et al. 1993). Restoration of airflow is straightforward in instances where solid walls or doors meant to prevent human entry are the cause, but impacts on bat populations are less straightforward than they may appear. Perhaps the most famous example comes from Wyandotte Cave, Indiana, where the winter population of Indiana bats increased by approximately 10,000 bats in the 14 years following removal of a stone wall at the cave entrance and installation of bat-friendly gates (Richter et al. 1993; Currie 2002; Johnson et al. 2002). Although cooling that occurred following elimination of the wall was credited as leading to this growth, counts from nearby hibernacula suggested Wyandotte Cave was the recipient of bats moving in from nearby sites, including sites where microclimates were presumed more favorable (Brack et al. 2003). Most notably, the population at Twin Domes Cave steadily declined following modification of Wyandotte Cave, despite Twin Domes Cave having cooler T_as within the range of temperatures "preferred" by Indiana bats (Richter et al. 1993; Tuttle and Kennedy 2002).

Although cooling hibernacula may be effective in some cases, we urge caution when basing management solely on adjusting the internal environment to supposed "optimal" temperatures. Such an approach will not always be successful; this is clearly shown by the results from Great Scott Cave (Elliott 2008), where reopening a blocked entrance did not yield a growth in population, as well as by other sites that go unused by bats despite suitable microclimates (Gore et al. 2012). Hibernacula microclimates are not the only factors driving habitat selection in winter, and management will only yield the desired response when underlying causes of low abundance or diversity are properly addressed (Fig. 13.2). Along with conditions inside hibernacula, the surrounding aboveground habitat is also likely to affect bats by influencing factors such as food availability and predation pressure. In Hungary, predation of hibernating common pipistrelles (*Pipistrellus pipistrellus*) by great tits (*Parus major*) decreased when food was provided for the tits (Estók et al. 2010), suggesting a link between habitat quality outside a hibernaculum to quality within. Habitat outside hibernacula may also influence availability of insect prey, which could benefit bats by providing increased foraging opportunities while bats are not hibernating. Finally, management at Wyandotte and Great Scott Caves focused on Indiana bats, and a single-species approach is unlikely to create suitable habitat for all cave-hibernating bats. This realization is essential for current management because another hibernating species, the northern myotis (*Myotis septentrionalis*), was recently listed as federally threatened in the United States and is considered endangered under Canada's Species at Risk Act, along with the little brown myotis and the tricolored bat.

Although restoring cool T_as does not always result in population growth, limited evidence suggests that cooling unused hibernacula with warm T_as can improve habitat in warmer regions. For example, state biologists in Pennsylvania created soil mounds to prevent cold air from flowing out of an abandoned mine with an entrance sloping uphill (Johnson et al. 2016). Prior to the arrival of WNS, an effort to trap cold air in the mine resulted in an increase in the number of hibernating little brown myotis and an increased species richness at the site. Other attempts to manage potential hibernacula similarly often go unpublished, although references to their success can be found in technical reports (Mitchell-Jones et al. 2007). Importantly, management such as this must be tailored to the local climate. For example, abandoned mines occupied by bats in Michigan's Upper Peninsula (46–47°N) are

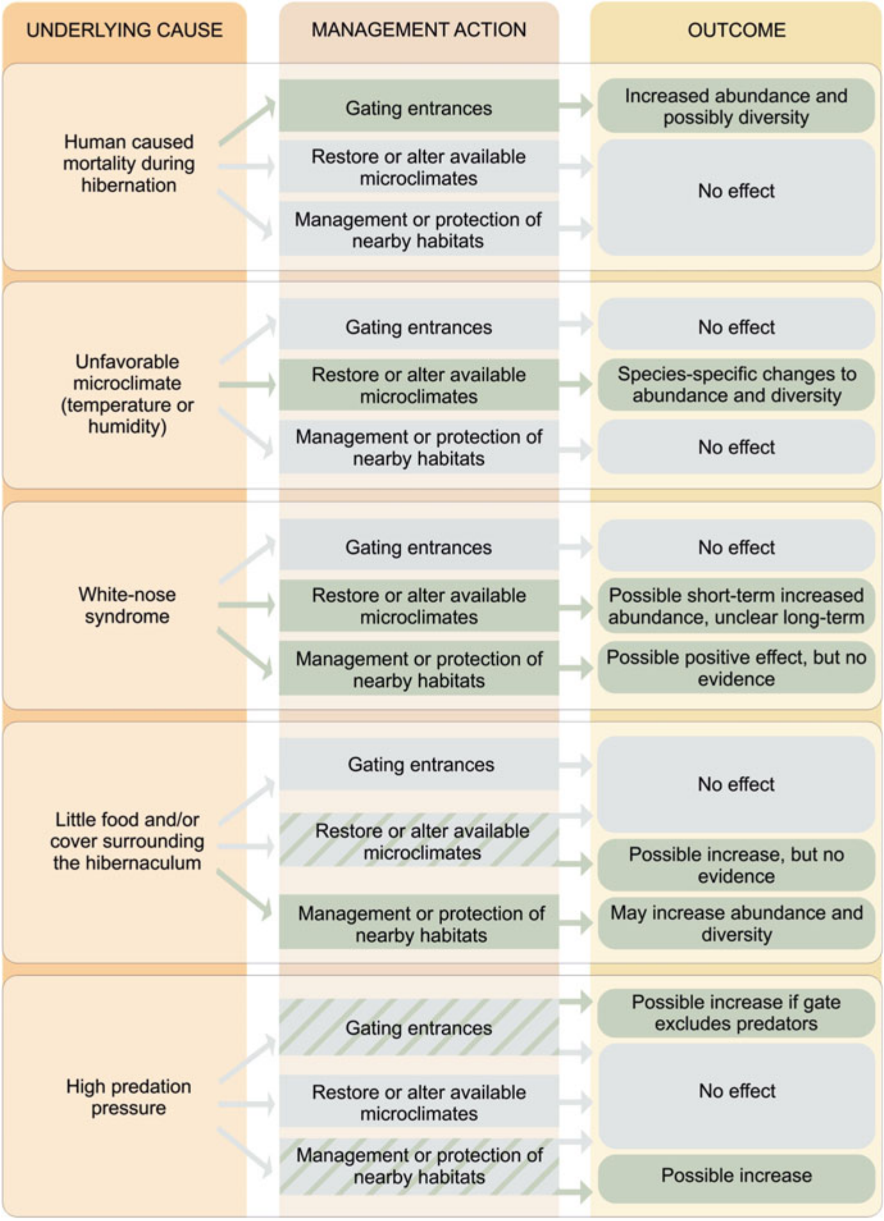

Fig. 13.2 Possible causes for low abundance or species diversity at hibernacula, along with expected outcomes of specific management actions that could be taken. Without identifying the underlying cause of low abundance or diversity at a site management may have no effect (gray shading) instead of the desired affect (green shading)

warmer than unoccupied sites, and creation of cold air traps would make the affected area uninhabitable by bats (Kurta and Smith 2014). Occupied sites in the Upper Peninsula lacked chimney-effect airflow that other studies found important (Tuttle and Kennedy 2002) and were more complex than unoccupied sites, likely with a wider range of microclimates available than mines without bats. Thus, although the importance of sites with warm or cold T_as varies latitudinally, hibernacula offering a diversity of thermal habitats are likely of high value at all latitudes.

The realization that hibernacula management is not as simple as maintaining or restoring specific T_as should not be surprising, given the need of bats to balance conflicting pressures described earlier. Unfortunately, WNS adds an additional variable to selection of winter habitat and further complicates management. Although many aspects of WNS have been reviewed (Frick et al. 2016), intersection of the disease with microhabitat selection and hibernacula management merits our attention. The fungus causing WNS, *Pseudogymnoascus destructans*, has a temperature-dependent growth rate, which is maximized between 12.5 and 15.8 °C, with rapidly decreasing rates at colder and warmer temperatures (Verant et al. 2012). Mortality of bats with WNS also varies with T_a in the hibernacula, with colder temperatures conferring a survival benefit (Langwig et al. 2012; Johnson et al. 2014; Lilley et al. 2016). In addition to being associated with slower fungal growth, low T_as likely benefit WNS-affected bats because cold temperatures promote increased use of torpor and limit arousals, as well as costly, potentially maladaptive immune responses (Lilley et al. 2017).

White-nose syndrome has, therefore, altered costs and benefits of hibernating at different T_as. The response of bats to this change can be used to test the hypotheses shown in Fig. 13.1, and potentially guide management. Specifically, a shift in habitat selection by both sexes towards colder T_as would broadly support the Hibernation Optimization Hypothesis, because bats would receive less benefit from minimizing torpor when suffering from WNS. Potentially more interesting, however, is whether females continue to select colder T_as than males, or if the negative effects of WNS are so great as to drive both sexes to similar microclimates. Finally, because the Colder is Better Hypothesis already predicts that bats select cold T_as, a corollary is that no shift in habitat selection should occur once bats become infected. Data from WNS-positive hibernacula in Pennsylvania show that remnant populations of little brown myotis, tricolored bats, and big brown bats (*Eptesicus fuscus*) have responded to the disease by moving to colder areas within sites (Johnson et al. 2016), thus refuting the Cold is Better Hypothesis, but sex-specific studies have not yet been conducted.

The shift in habitat selection by bats in response to a non-native species raises questions over how the need to increase short-term survival impacts long-term fitness. This trade-off has been shown in non-bat systems. For example, the behaviors that eastern fence lizards (*Sceloporus undulatus*) use to avoid predation by non-native fire ants (*Solenopsis invicta*) make the lizards more visible to avian predators (Thawley and Langkilde 2017). Similarly, a behavioral adaptation by bats to WNS may also have an associated price. Such trade-offs are critical to consider in management practices; although protecting cold hibernacula or cooling warm hibernacula may yield short-term benefits for survival in WNS-affected areas, overwintering at cold T_as comes at a physiological cost that might decrease long-term survival and reproduction. Finally, because different species select different T_as during hibernation (Brack 2007; Kurta and Smith 2014; Johnson et al. 2016), and individuals do not necessarily show a consistent preference throughout winter (Ryan et al. 2019), it is unlikely that management for narrow hibernacula conditions will meet with success in the years ahead. Careful consideration of the life history of hibernating bats in an area, availability of thermal habitats, and costs and benefits of hibernating across this range of conditions, are needed if hibernacula management is to succeed in mitigating WNS mortality.

13.4 Conclusion and Future Directions

Winter is a complex and dangerous time for cavernicolous species. At temperate latitudes, most species are obligate hibernators that migrate not in search of warmer climates, but of suitable hibernacula. Hibernating bats are not dormant until spring, but are periodically active to copulate, to reduce negative physiological consequences of torpor, and to select appropriate microclimates. This habitat selection is driven by factors both internal (e.g., physiology) and external (e.g., availability) to animals and to interactions among these factors that are not fully understood. Our review of what is known draws significantly on research presented and planned at NASBR over the past 50 years, and illustrates a clear shift from conceptualizing hibernation as a simple process geared towards conservation of energy toward a dynamic period during which bats balance costs and opportunities depending on their limited energy reserves.

Unfortunately, the need to fill remaining gaps in our knowledge of winter habitat selection by North American bats has been made more urgent by the arrival of WNS. Carefully designed experiments are needed to understand better the causes and consequences of winter habitat selection of cave-hibernating species and to determine how to modify hibernacula management in WNS-affected regions. Correlative studies, while valuable, are inherently limited in inferential scope and will never fully explain how conditions in hibernacula affect hibernating bats. In the absence of well-designed manipulative experiments, we run the risk of once again viewing winter habitat selection one-dimensionally, only this time through the lens of WNS. Similarly, while our summary focused extensively on temperature, the influence of factors such as humidity and airflow on habitat selection and WNS mortality must be better understood and incorporated into management. Finally, studies of alternative hibernacula are needed. Bats such as the eastern small-footed (*Myotis leibii*) and northern myotis appear to hibernate in rock crevices or rock piles (Lemen et al. 2016; Moosman et al. 2016; Weller et al. 2018) in addition to caves and mines, and even western populations of little brown myotis may rely on sites not traditionally considered hibernacula and are mostly inaccessible to humans (Lemen et al. 2016; Moosman et al. 2016; Neubaum 2018). Use of nontraditional hibernacula is poorly understood, but this behavior may be associated with different disease dynamics, and it certainly will require different management approaches.

When Humphrey presented his work on Indiana bats in 1975, disruption of hibernacula temperatures and human disturbance were the greatest threats to North American bats during winter. Nearly 50 years later, the role of temperature during winter remains a central focus of winter research and management. Successful management will require that wildlife professionals avoid returning to our previous, over-simplified understanding of the role of temperature, and that we expand our understanding of other aspects of winter habitat selection. To continue to grow our understanding of winter habitat selection, we emphasize the need for experimental studies and investigations of physiological, ecological, and fitness consequences of habitat selection at different T_as beyond just energy conservation.

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Chapter 14
Torpor and Tinbergen: Integrating Physiological and Behavioral Traits with Ontogeny, Phylogenetic History, Survival and Fitness to Understand Heterothermy in Bats

Yvonne A. Dzal, Allyson K. Menzies, Quinn M. R. Webber, and Craig K. R. Willis

Abstract The importance of connecting physiological, behavioral, and life-history traits with evolutionary outcomes has long been recognized by biologists and was perhaps most elegantly formalized in Tinbergen's (Z Tierpsychol 20:410–433, 1963) four-question framework. What are the mechanisms associated with a trait? How does the trait develop over an individual's lifetime? What is the phylogenetic context of the trait? And finally, often the most difficult to answer, what are the fitness implications of the trait? This framework was developed to understand behavior and rarely has been applied in other fields, despite its potential to inform our understanding of many biological phenomena. Niko Tinbergen and colleagues were awarded a Nobel Prize in 1973 just after the first North American Symposium on Bat Research (NASBR), and since then, Tinbergen's framework has become second nature to researchers studying bat behavior. However, it is under-used for studying other aspects of bat biology. Thus, in honor of 50 years of NASBR, we use studies on heterothermy and hibernation in bats to highlight the value of Tinbergen's four questions for research in physiology. We conclude by addressing the

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implications of an integrative Tinbergen-like approach for addressing conservation threats to bats, with emphasis on research concerning white-nose syndrome, much of which was first presented at NASBR meetings.

Keywords Ecological energetics · Heterothermy · Integrative research · Physiology · White-nose syndrome

14.1 Introduction

The importance of connecting physiological mechanisms with behavioral, ecological, and evolutionary outcomes has long been recognized by biologists. These connections were elegantly formalized in Tinbergen's (1963) four-question framework developed to provide a comprehensive understanding of the evolution of behavioral traits. What physiological and behavioral processes or mechanisms underlie a specific trait? How does the trait develop over an individual's lifetime? What is the phylogenetic context of the trait? And finally, the question that is often the most difficult to answer for free-living animals, what are the survival and fitness implications of the trait? Tinbergen (1963) proposed this framework while pioneering the field of ethology; it has been most commonly applied in animal behavior (e.g., Davies et al. 2012), with less influence on other fields, despite its potential to provide an integrative understanding of many different types of traits and biological phenomena (but see Bateson and Laland 2013).

Animal physiology is one example of a field that, despite potential benefits, has not fully embraced Niko Tinbergen's framework. For much of the twentieth century, studies in comparative physiology emphasized mechanistic questions, with some focus on phylogenetic context (hence *comparative* physiology) and the ontogeny or development of traits. However, in contrast to studies in animal behavior (Bateson and Laland 2013), comparative physiology research has rarely linked these questions to data on survival or fitness. In part, this reflects logistic constraints because often the equipment needed to study physiology is not suited to field conditions. Physiologists may also be less likely than behaviorists to integrate research on mechanisms with estimates of fitness because of the theoretical underpinnings of their respective fields. Tinbergen's four questions are foundational for most undergraduate courses and textbooks in animal behavior (e.g., Davies et al. 2012; Rubenstein and Alcock 2019) and are second nature to behaviorists, but the questions are usually absent from physiology curricula (e.g., Sherwood et al. 2012; Moyes and Schulte 2016). Thus, studies connecting physiological traits of individuals with real-world survival and fitness are rare, limiting our understanding of how biotic and abiotic factors in the environment influence animal biology.

Recognition of the limits of laboratory studies alone to inform our understanding of organismal function has been a growing trend for interdisciplinary research that blurs the lines between physiology, behavior, ecology, and evolution (e.g., Speakman et al. 2003). Unlike traditional comparative physiology, ecophysiology and ecological energetics have used technological advances combined with integrative approaches to study physiological and behavioral patterns in the field, in the context of real-world environmental constraints (Tomlinson et al. 2014). Likewise, the growing applied field of conservation physiology combines theory, questions, and techniques from across disciplines to understand responses of animals to environmental change and inform management and conservation strategies (Wikelski and Cooke 2006).

Heterothermy is an ecologically important aspect of mammalian biology, especially among bats, that is well suited to an integrative, Tinbergen-like approach. Unlike homeotherms that maintain a relatively constant body temperature (T_b) independent of ambient temperature (T_a), heterotherms can reduce T_b and metabolic rate to save energy (Lyman 1970; Geiser 2004). Facultative heterotherms can reduce T_b and metabolic rate at any time of year, especially when confronted with energetic stressors such as low T_a or limited food or energy reserves, whereas torpor use in obligate heterotherms may only be seasonal (hibernation) (Geiser 2004; Ruf and Geiser 2015).

Virtually all aspects of the ecology of temperate endotherms are affected by the energetic bottleneck of winter (i.e., high energetic costs, low food availability), and this bottleneck is especially obvious for hibernators. Hibernation is defined as the prolonged and seasonal use of torpor, characterized by extensive reductions in T_b and metabolic rate, but it also involves significant pre-winter energy storage, precise microhabitat selection and, sometimes, migration between summer and winter habitats (e.g., Geiser 2004; Boyles et al. 2007; Norquay et al. 2013; Fig. 14.1a). Hibernation is also intimately linked with life-history and ecological traits, including reproductive timing (Bieber et al. 2012), lifespan (Wilkinson and South 2002; Turbill et al. 2011), social behavior (Boyles and Brack 2009), and geographic distribution (Humphries et al. 2002). Thus, while many studies have quantified physiological mechanisms associated with heterothermy in laboratory conditions, fully understanding this phenomenon requires an integrative approach incorporating theory and techniques from physiology, behavior, ecology, and evolutionary biology (Fig. 14.1).

Despite the value of integrative research, our understanding of heterothermy and hibernation in free-ranging bats has been constrained by boundaries between disciplines. Nevertheless, at the first North American Symposium on Bat Research (NASBR) in 1970, Eugene Studier and Michael O'Farrell highlighted the value of integrating laboratory studies of physiology with data on natural history and behavior, and this work stimulated bat research with a clear Tinbergen-like, integrative approach. Their subsequent work (Studier and O'Farrell 1972; Studier et al. 1973; O'Farrell and Studier 1973, 1975, 1976; Studier and O'Farrell 1976) pioneered a body of literature that enhanced understanding of the ecophysiology of free-ranging bats (e.g. McNab 1982; Speakman et al. 2003). Coincidentally, Tinbergen (with Karl von Frisch and Konrad Lorenz) received the Nobel Prize in Physiology and Medicine for their pioneering work in the study of animal behavior in 1973, shortly after the first NASBR. Thus, the historic context of early NASBR meetings included new

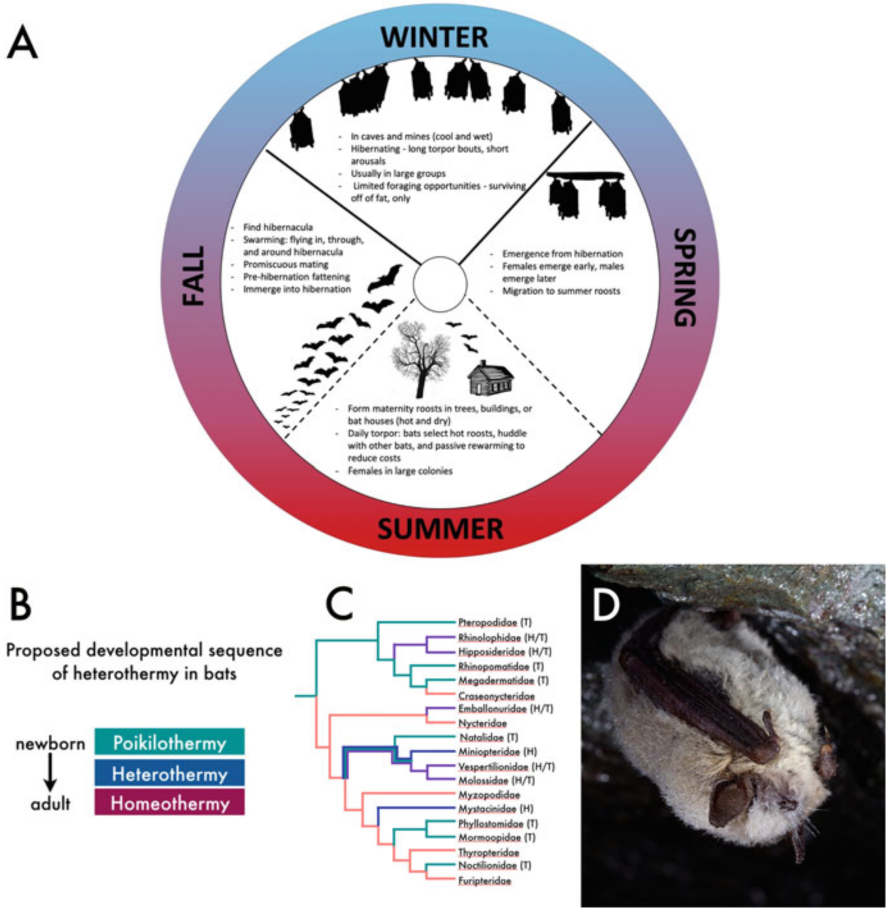

Fig. 14.1 Using Tinbergen's four questions for a comprehensive, multifaceted understanding of the ecological energetics of heterothermy in bats. Despite Tinbergen's emphasis on the need for an integrated understanding, all four questions have been addressed in few systems. One fascinating, ecologically important system with potential to be illuminated by integrative ecophysiological research is heterothermy in bats. (**a**) **Mechanism.** Researchers have amassed a good understanding of the physiological, behavioral, and ecological processes underlying heterothermy that drive the seasonal ecology of temperate hibernating species. Taken together, these studies introduce the complex interactions among ambient temperature, microclimate selection, sex, and huddling behavior, which exemplify the physiological and behavioral flexibility involved in bat thermoregulation. (**b**) **Development.** Ontogenetic investigations have revealed that heterothermy could be a critical energy-saving strategy used by many altricial mammals throughout postnatal development, allowing newborn mammals to allocate energy into growth and development, rather than thermogenesis during adverse conditions. Although torpor use has been documented in juvenile and adult bats, the ontogenetic sequence of heterothermy is largely unknown. (**c**) **Evolution.** Comparative analyses have established that heterothermy in bats is common and widely distributed among phylogenetic lines, with 14 out of 19 bat families exhibiting heterothermy. These studies suggest that the most parsimonious phylogenetic history of thermoregulation in bats is that the ancestors of bats were in fact heterothermic. Branches show families with species that are homeotherms (coral), facultative heterotherms (teal; torpor (T)), seasonal heterotherms (blue;

recognition, via the most important prize in science, of the value of integrative research, and Tinbergen's framework for studying animal biology.

Our goal for this chapter is, therefore, to use studies on the ecological energetics of hibernation and daily heterothermy to highlight the value of Tinbergen's four questions for a comprehensive understanding of physiological traits of bats (Fig. 14.1). Following Tinbergen's framework, we examine conceptual and empirical developments and highlight how work since 1970, much of it by NASBR attendees, has contributed to a more integrative understanding of hibernation and heterothermy. We focus primarily on temperate-zone hibernating species because their dependency on seasonably variable insect prey, ability to survive in highly variable environments, and energetically expensive mode of locomotion make them a valuable model for studying energetics. We conclude by addressing how quantifying survival and fitness and answering Tinbergen's fourth and most challenging question for free-ranging bats can enhance our understanding of bat biology and provide crucial information for conservation in an era of unprecedented threats to bats.

14.2 Tinbergen's Four Questions Applied to Hibernation and Heterothermy in Bats

1. What are the Physiological and Behavioral Mechanisms Underlying Prolonged Heterothermy in Bats?

Much of the early work on heterothermy and hibernation in bats focused primarily on quantifying physiological variables in the laboratory, including reductions in T_b, heart rate, respiratory rate and, ultimately, metabolic rate and evaporative water loss (Twente et al. 1985; Thomas 1993). Torpor during hibernation is characterized by extreme reductions of T_b to near T_a, controlled reductions of metabolic rate to 1% of resting metabolic rate, and slowing of other physiological processes, such as heart rate and respiratory rate, to minimal levels (Geiser 2004; Ruf and Geiser 2015). Dramatic reductions in physiological parameters result in tremendous energetic savings that allow some hibernators to remain inactive for months without feeding (Geiser et al. 1990; Czenze et al. 2013), and survive on less than a gram of fat for up to 200 days of hibernation (Thomas et al. 1990; Thomas and Cloutier 1992). If bats,

Fig. 14.1 (continued) hibernation (H)) or both facultative and seasonal heterotherms (purple). Figure modified from Yuan et al. 2011. (**d**) **Survival and Fitness**. Heterothermy is a significant factor in explaining variation in longevity among bat species and has likely been a key survival strategy for many species throughout their evolutionary history, due to long periods of inactivity in a sheltered roost, reduced forging requirements, as well as reduced starvation and predation risk associated with heterothermy (photo of hibernating *Myotis lucifugus* courtesy of Brock Fenton) instead, maintained a high and constant T_b, their fat reserves would support their energetic requirements for less than one month (Humphries et al. 2004).

Torpor saves energy, but hibernation is not a continuous steady state and, throughout winter, hibernators arouse from torpor at regular intervals, increasing T_b and metabolic rate to normothermic levels, for minutes to hours (Speakman and Racey 1989; Thomas et al. 1990). While arousals from torpor are brief and typically represent only 5–10% of the winter time budget, they account for up to 90% of energy expenditure during hibernation (Thomas et al. 1990; Jonasson and Willis 2012). The fact that these energetically costly arousals are near universal for mammalian hibernators suggests that they serve important functions; likely playing a role in allowing hibernators to excrete metabolic wastes that accumulate during torpor bouts, rehydrate after water loss during prolonged torpor, and possibly restore immune function (Thomas and Cloutier 1992; Thomas and Geiser 1997; Burton and Reichman 1999).

A growing body of literature, much of it on bats, demonstrates that hibernators do not necessarily express the longest, deepest bouts of torpor of which they are capable to save energy. Instead, individuals that have sufficient energy reserves appear to avoid prolonged deep torpor, presumably to minimize torpor's physiological costs (Humphries et al. 2003; Jonasson and Willis 2011; Johnson et al. 2021). While some hibernators store food, this is not an option for temperate bats, and their torpor patterns are determined by the size of their pre-hibernation fat stores. With little or no flexibility on the income side of the winter energy budget, temperate hibernating bats must tightly regulate expenditure and optimize torpor expression (Thomas et al. 1990; Jonasson and Willis 2011; Czenze et al. 2017).

Although hibernacula are often thermally stable, spatial variation in T_a, humidity, light exposure, and other abiotic factors occur and can influence hibernation patterns (Boyles et al. 2007). Individuals with abundant energy stores can reduce depth and duration of torpor bouts by hibernating at warmer T_a within their hibernacula, which can minimize adverse effects of prolonged torpor. Bats with small energy reserves may incur greater physiological costs from using deep torpor, but by hibernating at colder rather than warmer temperatures, they can use deeper torpor, which leads to greater energy savings and increases overwinter survival (Boyles et al. 2007; Johnson et al. 2021). Temperate hibernating bats also select their overwintering sites based on humidity (Ben-Hamo et al. 2013), and optimal levels of hibernacula humidity differ both within and between species. Unfortunately, studies investigating microsite selection by temperate hibernating bats are rare, and most studies have reported relative rather than absolute humidity, which is biased by temperature (Kurta 2014; Johnson et al. 2021).

Due to differences in the timing of reproductive investment, males and females differ in their overwintering thermoregulatory strategies (Jonasson and Willis 2011; Czenze et al. 2017). For females, minimizing arousals and using deep, prolonged torpor during hibernation can conserve resources for allocation to reproduction in the spring (Jonasson and Willis 2011; Czenze et al. 2017). Males, on the other hand, do not face the burden of reproductive investment in spring and mitigate physiological costs of prolonged torpor via shallower torpor bouts and longer-duration arousals than females (Jonasson and Willis 2011; Czenze et al. 2017). Males mate with torpid females during hibernation (Thomas et al. 1979), which may also explain prolonged arousals of males (Jonasson and Willis 2011; Czenze et al. 2017). By linking torpor use and the energetic costs associated with hibernation to differences in individual body condition and sexual differences in the timing of reproduction, these studies have helped reveal interactions among physiological, behavioral, and life-history mechanisms that define bat hibernation (Fig. 14.1a).

As physiological research has become more common in the field, where animals can express a full range of behavioral variation, it has become clear that mechanisms facilitating heterothermy and hibernation in bats also involve social behavior (Boyles et al. 2008; Czenze et al. 2013; Boratyński et al. 2015; Fig. 14.1a). As early as the 1950s, the link between huddling and thermoregulation in hibernating bats was documented based on evidence that social species selected cooler microclimates than solitary species (Beer and Richards 1956), had smaller clusters in warmer caves than in cooler sites (Twente 1955), and tended to huddle less in mild vs. cold weather (Hooper and Hooper 1956). By the 1970s, Studier and colleagues (Procter and Studier 1970; Studier 1970) suggested that huddling also lessened water loss for normothermic bats. More recent work has confirmed that huddling during hibernation is an active behavioral process that reduces evaporative water loss in bats (Boratyński et al. 2012, 2015) and decreases heat loss during arousals from hibernation (Boyles et al. 2008). Thus, for bats, social thermoregulation during hibernation can provide substantial energetic savings, due to reduced need for metabolic heat production, and allows bats to exploit drier sites than solitary individuals without incurring additional energetic costs (Thomas and Cloutier 1992). More work is needed but, taken together, these studies have helped answer Tinbergen's first question about mechanisms involved in hibernation and heterothermy, by characterizing the influence of physiological traits (e.g., T_b and metabolic rate regulation, water loss), life-history characteristics, sexual differences, and behavioral traits (e.g., huddling, microclimate selection) on the expression of torpor and hibernation (Fig. 14.1a).

2. How Does Heterothermy Develop over the Lifetime of Individual Bats?

Information on torpor use during postnatal development is available for only ~0.1% of extant endotherms (less than 15 species of mammals and birds) (Geiser 2008; Geiser et al. 2019; Renninger et al. 2020). Bats, like most endotherms, are born altricial and mostly hairless, with little subcutaneous fat and little ability to produce heat through shivering thermogenesis (O'Farrell and Studier 1973; Hollis 2004). Their lack of insulation, large ratio of surface area to volume, and poor thermogenic capacity make newborn bats susceptible to rapid heat loss. As bats mature, however, the ratio of surface area to volume decreases, while their fur and nervous system develop, collectively improving their thermoregulatory ability a few weeks after birth (Reynolds and Kunz 2000; Hollis 2004). Nevertheless, juvenile bats, with their smaller body size, still have higher rates of heat loss than adults, and selection likely favors use of heterothermy during development, since torpor can help small-bodied juveniles save energy during periods of energetic constraint (e.g., when food is limited) and/or periods of rapid heat loss (e.g., when the mother leaves the roost to forage). While prolonged torpor can slow growth and development (Racey 1973; Wilde et al. 1999), optimizing when torpor is used and/or avoided could allow juveniles to allocate more energy to growth, development, and maintenance (Giroud et al. 2012), rather than to energetically expensive thermogenesis (Geiser and Brigham 2012).

Differentiating uncontrolled heterothermy (i.e., poikilothermy from which individuals cannot spontaneously arouse) from controlled heterothermy or torpor (i.e., from which metabolic heat production enables arousal) is critical for understanding the ontogeny of heterothermy (Geiser 2008; Geiser et al. 2019; Renninger et al. 2020; Fig. 14.1b). In the only comparative investigation of the development of T_b regulation and heterothermy in small endotherms (marsupials, placental mammals, and birds), Geiser (2008) reported two different developmental sequences for heterothermy. All endotherms Geiser investigated were poikilothermic at birth (Fig. 14.1b), with T_b and metabolic rate decreasing linearly with T_a. In birds and marsupials, T_b regulation and controlled heterothermy developed immediately after poikilothermy (Geiser 2008). However, in placental mammals, poikilothermy was immediately followed by the ability to regulate only normothermic T_b, and controlled heterothermy did not develop until weeks or even months after birth (Geiser 2008). Recent studies on additional placental mammals—the desert hamster (*Phodopus roborovskii*) and house mouse (*Mus musculus*)—found the same heterothermic developmental sequence as that in birds and marsupials (i.e., immediate development of controlled heterothermy) (Geiser et al. 2019; Renninger et al. 2020). These data provide some insight into how controlled heterothermy develops in endotherms, generally, but more detailed investigation of torpor use throughout postnatal development is needed, especially for bats.

3. What is the Phylogenetic Context of Heterothermy in Bats?

There are over 1,400 species of bats, with heterothermic species widely distributed within most (14) of the 19 families (Teeling et al. 2005; Yuan et al. 2011; Fig. 14.1c). Bats occupy diverse habitats and exhibit a range of thermoregulatory patterns, providing a good opportunity to study the evolutionary history and phylogenetic context of heterothermy and hibernation. Historically, subtropical and tropical bats were considered strict homeotherms (Stawski et al. 2014), but torpor has now been documented in many of them (Geiser et al. 2011; Stawski and Geiser 2012), emphasizing that torpor in bats is not restricted to species living in cold or temperate climates. Although considerable information exists on morphological, physiological, and behavioral characteristics associated with heterothermy (see Sect. I and II), its evolutionary origin is still unresolved (Yuan et al. 2011).

There are three hypotheses about the evolution of heterothermy in bats (Geiser 2008). The first is that hibernation is an ancestral trait, reflecting a temperate origin for bats, with torpor expression reduced or lost in multiple lineages as bats colonized subtropical and tropical environments (Yuan et al. 2011). The second is that bats evolved in subtropical or tropical environments, where short-term heterothermy was beneficial during periods of energetic shortfalls. Then, as bats diverged and colonized temperate environments, short-term heterothermy evolved into hibernation in some species while being lost in some tropical species. In this scenario, hibernation and strict homeothermy are both derived states (Yuan et al. 2011). The third is that ancestral bats were homeothermic and that heterothermy evolved independently in multiple lineages, when bats colonized more variable and colder temperate environments, although this scenario seems unlikely, given that homeothermy is rare in extant bats (Yuan et al. 2011).

Available data are consistent with the view that the common ancestor of bats was heterothermic and that heterothermy was lost in multiple lineages because of favorable climates and abundant food (Geiser and Stawski 2011). Also, heterothermy in mammals has not been associated with the emergence of novel genes (Carey et al. 2003). Thus, it is conceivable that the genetic basis of heterothermy is common to the mammalian genome and that variation in the expression of such genes may provide the basis for the degree of heterothermic expression observed among mammals, including bats, from homeothermy at one extreme to long-term deep torpor and hibernation at the other.

4. Tinbergen's Toughest Question: What are the Survival and Fitness Implications of Heterothermy in Bats?

Tinbergen's fourth question concerns the survival and fitness implications of particular traits. Perhaps the most powerful way to address it is to quantify traits among individuals and correlate these traits with estimates of fitness for the same individuals but such data are scarce, likely due to the challenge of quantifying survival and fitness for bats. Nevertheless, the importance of heterothermy and hibernation to survival and fitness of bats seems indisputable (Turbill et al. 2011). Bats are generally longer lived than similar-sized mammals, and heterothermic bats live significantly longer than homeothermic species (50% longer for a 50-g species), with several records of heterothermic bats surviving more than 30 years in the wild (Wilkinson and South 2002; Turbill et al. 2011; Fig. 14.1d). Rate-of-living theory states that longevity is influenced by metabolic rate, with fast metabolic rates, rapid growth, and high reproductive rates correlated with a short lifespan (Pearl 1928). Consistent with rate-of-living theory, heterothermic bats are longer lived than homeotherms, possibly because heterothermy allows metabolic rate to slow (i.e., during torpor and hibernation) and, consequently, reduce damage from toxic metabolic by-products that accumulate with age (Wilkinson and South 2002). In addition to reducing long-term effects of aging, heterothermy may help bats avoid other sources of mortality, such as accidents and predation, by allowing them to reduce time spent foraging (Nowack et al. 2017). Interestingly, heterothermy may have been critical for survival of small mammals during the mass extinctions at the Cretaceous-Paleogene boundary (Lovegrove 2019), which primarily involved homeothermic species (Geiser and Turbill 2009).

While there is indirect evidence that heterothermy increases survival and lifespan for bats, few empirical data connect variation in heterothermy with individual-level survival and fitness. Boyles and Brack (2009) used individual-based models of energy expenditure to estimate effects of arousal frequency, clustering, and environmental conditions on survival rates of hibernating bats. They showed that more frequent arousals can increase the probability of mortality, although their models also suggest that most bats store enough fat to tolerate 'extra' or unpredictable arousals (e.g., due to disturbance by potential predators). Fully understanding individual survival and fitness, however, requires the ability to follow individuals in the wild, which is clearly a challenge for bats.

Many studies have used forearm bands (Keen and Hitchcock 1980; Kunz 1996; Frick et al. 2010) and, more recently, passive integrated transponders (PIT) to quantify annual survival of free-ranging bats (O'Shea et al. 2004; Frick et al. 2010). To our knowledge, none of these studies has connected individual survival with variation in physiological or behavioral traits associated with heterothermy and hibernation, but they have shed light on the influence of demographic parameters and environmental conditions on survival (e.g., O'Shea et al. 2004; Frick et al. 2010). Long-term mark-recapture datasets for bats are rare but these have the greatest potential to connect variation in hibernation physiology and behavior with individual- or population-level survival. For example, Norquay and Willis (2014) used a PIT-tag reader at the entrance of a hibernaculum to quantify immergence and emergence phenology of individuals. Longer-term, multi-year datasets combining this approach with mark-recapture analyses could help connect variation in phenology with individual survival. Combining technologies could also be useful, for example, by quantifying arousal frequency and duration using temperature-sensitive radio-transmitters with PIT tags to quantify phenology and survival of the same individuals (Czenze and Willis 2015).

Although studies of survival in bats are uncommon, rarer still are those quantifying reproductive fitness, because this requires the ability to determine individual reproductive success. This is extremely challenging for most bats but, in our view, worth pursuing. It may not be feasible to quantify individual reproductive success in the wild for many species, but it may be possible to do so for bat colonies as a whole. For example, we can quantify proportions of females that are reproductive in a colony along with capture rates of juveniles and ratios of adults to juveniles (e.g., Lentini et al. 2015; Gager et al. 2016). These reproductive rates could then be compared among colonies that vary in physiological or behavioral traits (e.g., Linton and MacDonald 2018), and, thus, help address the evolution of traits important for heterothermy and hibernation across large temporal or spatial scales (e.g., phenological, latitudinal, or elevational gradients). However, creative approaches to quantifying reproductive success and addressing Tinbergen's toughest question for bats are still needed for a complete understanding of the survival and fitness implications of heterothermy in bats.

5. Applying Tinbergen's Framework to Bat Conservation: Insights from White-Nose Syndrome

Bats currently face many conservation threats (Voigt and Kingston 2016) and integrative research that includes tackling Tinbergen's toughest question can strengthen conservation research and provide new insights for population management. The fungal skin disease, white-nose syndrome (WNS), is a devastating conservation threat for multiple hibernating bat species, which has killed millions of bats across North America since its discovery in New York State in 2006 (Frick et al. 2015). Skin infection with *Pseudogymnoascus destructans*, the causal fungus, results in lesions, disrupts hibernation physiology and behavior, and negatively affects water balance, thermoregulation, and gas exchange (Cryan et al. 2010; Warnecke et al. 2013; Verant et al. 2014). This pathophysiology causes increased arousal frequency and energy expenditure during hibernation, premature depletion of fat stores, and, ultimately, death. Nevertheless, just over ten years after the WNS outbreak, some populations appear to be stabilizing or rebounding, and several mechanisms underlying this stabilization have been proposed and are being tested (Frick et al. 2017; Langwig et al. 2017; Cheng et al. 2019; Auteri and Knowles 2020).

Although studies of WNS have not referred explicitly to Tinbergen's framework, a Tinbergen-like approach, applied to physiological traits and pathophysiology, has been useful for understanding WNS and devising potential management actions, with some of this work first presented at NASBR. The first priorities for addressing WNS have been to answer Question 1 and characterize disease pathophysiology (e.g., Blehert et al. 2009; Verant et al. 2014) and to answer Question 2 by quantifying progression of the disease over time (i.e., its development) (e.g., Warnecke et al. 2012). Understanding phylogenetic context and addressing Question 3 have been important for helping reveal the Eurasian origin of *P. destructans* (e.g., Puechmaille et al. 2011) and could be crucial for understanding variation in susceptibility to WNS among species. Finally, addressing Tinbergen's toughest question, Question 4, has been important for understanding the scale of WNS impacts and potential management responses. Several studies have used models or indirect estimates of survival (e.g., counts of bats in hibernacula) to suggest links between hibernation traits, aspects of the host-pathogen interaction in WNS, and bat survival (Maslo and Fefferman 2015; Verant et al. 2018). A number of studies have also directly connected empirical measurements of individual traits (or aspects of the WNS host-pathogen interaction) with survival (e.g., Reeder et al. 2012; Warnecke et al. 2012). Accumulating evidence suggests that some physiological traits differ among individuals and species that are WNS-susceptible versus WNS-tolerant/resistant (Cheng et al. 2019). In particular, the species that are most affected are particularly susceptible to increases in water loss or energy expenditure (Willis et al. 2011). Cheng et al. (2019) demonstrated that some individuals persisting after WNS had larger fall fat stores than animals from before WNS invasion, and that these higher fat stores could reduce WNS mortality by 58% to 70%. If body condition is important for WNS survival, then protecting and enhancing critical foraging habitats to provide food for bats in fall could be an important management action to help bats prepare for hibernation and help bats recover from WNS. Although none of these studies explicitly refer to Tinbergen, they highlight the value of Tinbergen's four questions, especially integrating an understanding of physiology with estimates of individual survival to tackle urgent conservation issues.

14.3 Conclusion

Although hibernation research has historically leaned toward quantifying physiological mechanisms, bat researchers, since the first NASBR, have highlighted the value of integrative approaches, and studies of hibernation and heterothermy illustrate this point. Integrating theory, questions, and hypotheses from historically distinct disciplines has improved our fundamental understanding, while enhancing the potential of physiological research to inform management and conservation. In the context of Tinbergen's questions, bat biologists have developed a good understanding of many of the proximate mechanisms associated with hibernation and heterothermy in bats, at least for adults of some species. Hibernation and heterothermy clearly result in dramatic energy and water savings, while also influencing a range of behavioral patterns like habitat selection and clustering with conspecifics. We know less about the ontogeny of heterothermy, and additional studies of bats throughout their development are needed to address Tinbergen's second question. Combining field studies with data from the few captive breeding colonies that exist could be useful in addressing this objective.

In terms of the ultimate causes and consequences of heterothermy and hibernation, Tinbergen's third question about the phylogenetic origin of heterothermy in bats is still not fully understood but the best evidence suggests that heterothermy is an ancestral trait. The diversity of bats and the widespread expression of heterothermy across the Chiroptera provide exciting opportunities to understand factors driving the evolution of heterothermy, or the tendency toward homeothermy, in endotherms generally. Perhaps the most important and most difficult, however, is Tinbergen's fourth question that requires determining survival and fitness implications of heterothermic variation within and across species. Creative approaches to overcome the logistical challenges of monitoring individual survival and especially reproductive success of individual bats across their lifetimes should be a crucial priority to improve our understanding of bats and to conserve and manage their populations in the face of urgent conservation threats like WNS.

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Part VII
Methods

Erin H. Gillam

Compared to other mammals, bats are notoriously difficult to study in natural environments, as their ability to achieve rapid flight coupled with their nocturnal nature make individuals hard to catch and follow for any length of time. While many new tools have arisen in the last 50 years, some of the core methods we rely on today were first coming into use in 1970 when the initial NASBR meeting was held. In this section, we look at two commonly used tools for studying bats—radiotelemetry systems for tracking the movements of bats across the landscape and the harp trap, a common tool for capturing bats. Even though both of these methods have been around for 50 or more years, their use has changed substantially over time.

In Chapter 15, Clerc et al. assess how the use of radiotelemetry systems has changed since they were first used to study bats in the late 1960s. The authors walk through a history of this technology and how it has been used to answer a variety of research questions. Specifically, the authors discuss a three-phase framework for understanding the evolution of radiotelemetry research. The initial phase, when use of the technology was new, allowed researchers to ask questions about the movement patterns of bats that previously were not possible to answer. As costs and transmitter masses decreased, radiotelemetry became an increasingly common method employed by biologists. Finally, use of this technology matured beyond asking questions focused solely on movement patterns to investigate other aspects of the biology of bats, such as physiology.

In Chapter 16, Tanshi et al. look at how the harp trap has been used in bat research around the world. The harp trap is a critical tool for studying bats, as it allows researchers to capture bat species that adeptly avoid mist nets. Unlike radiotelemetry, the basic harp trap has remained relatively unchanged in design since it was first introduced in 1958, with the most recent major structural modifications occurring in

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the late 1980s. Tanshi et al. discuss how use of the harp trap around the world has contributed to our understanding of global bat diversity. The authors discuss how the amount of harp trap use has changed over time, as well as the regions of the world where this method is particularly important for describing bat communities and identifying new species.

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

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

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

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

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

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

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

15.1 A Framework for Considering the History of Radiotelemetry and Bats

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

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

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

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

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

15.2 Data Collection

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

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

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

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

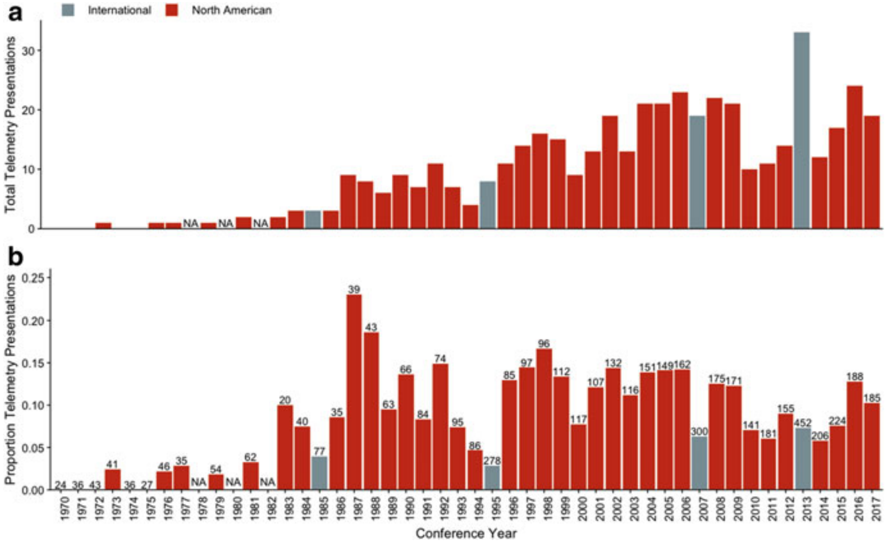

Fig. 15.1 (**a**) Number of presentations at NASBR that involved radiotelemetry. (**b**) Proportion of presentations in each year that involved radiotelemetry. Total number of presentations each year is included atop each bar. International refers to years when NASBR held joint meetings with the International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

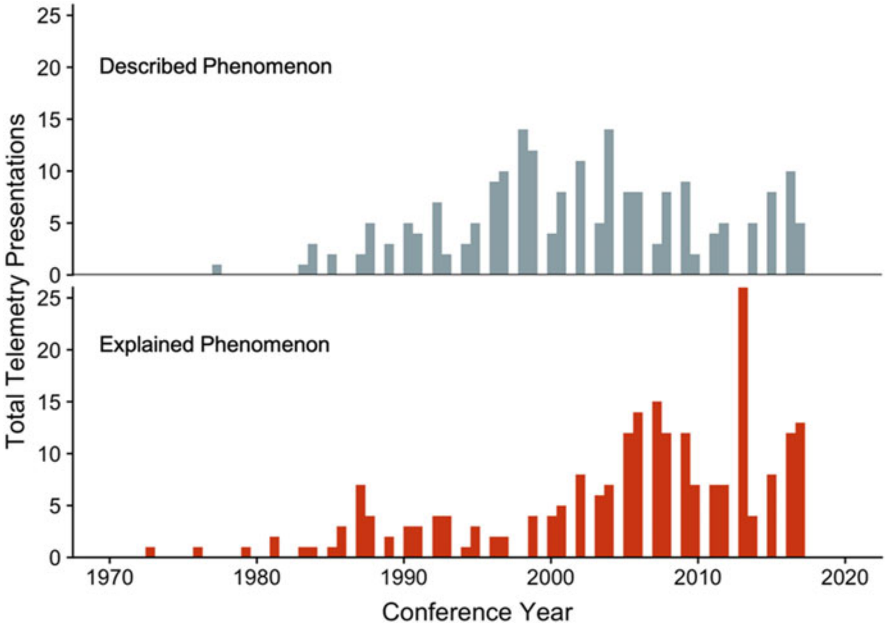

Fig. 15.2 Number of NASBR presentations through time, representing hypothesis-driven presentations (explained phenomenon) and natural history presentations (described phenomenon)

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

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

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

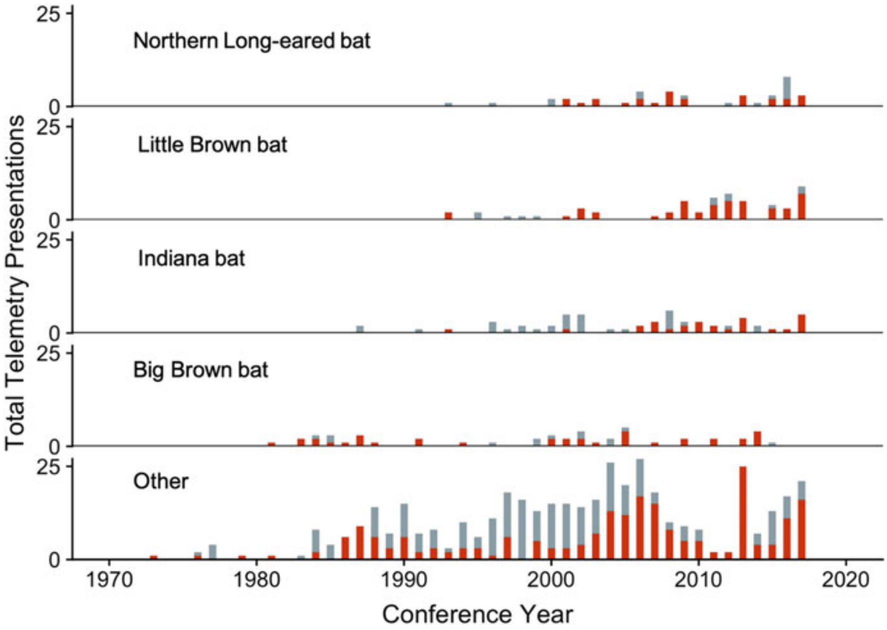

Fig. 15.3 Presentations at NASBR related to species that have more than 30 occurrences in the dataset. Red bars represent hypothesis-driven presentations (explained phenomenon) and grey bars represent natural history presentations (described phenomenon)

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

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

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

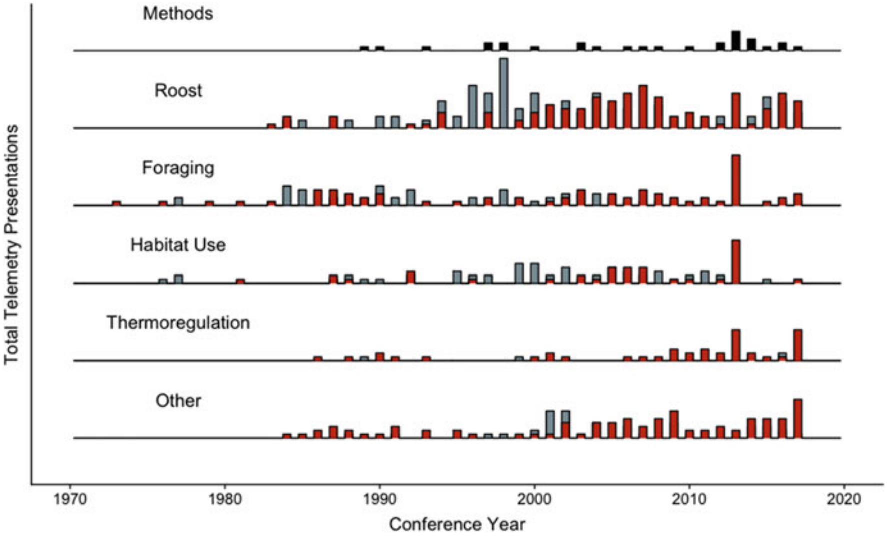

Fig. 15.4 Subject of radiotelemetry presentations by year at NASBR. Methodological presentations first appeared in 1989 and have since been a regular feature. Our main analysis focused on presentations of biological questions and observations with dependent variables including roost, foraging, habitat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

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

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

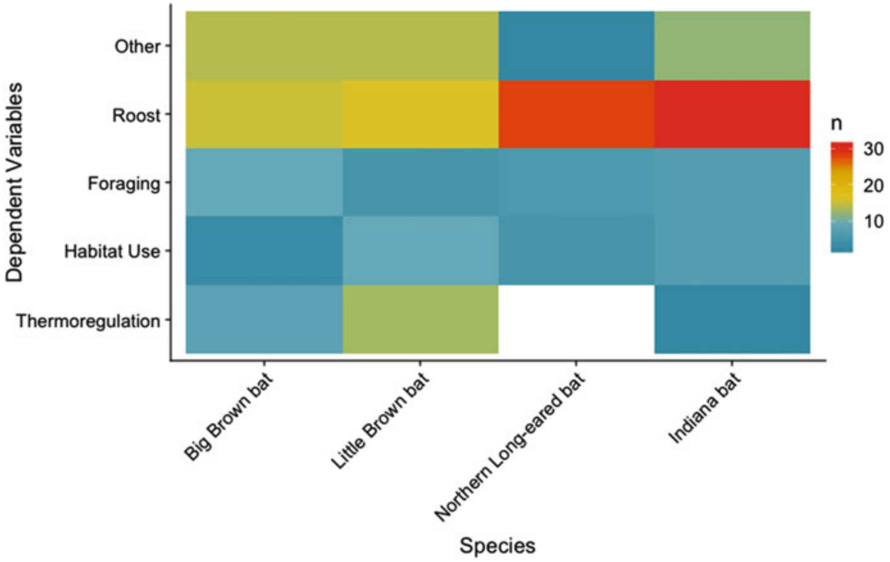

Fig. 15.5 Heat map representing the number of times a topic and species occur together in the dataset, focusing on species that are referenced over 30 times in the dataset

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

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

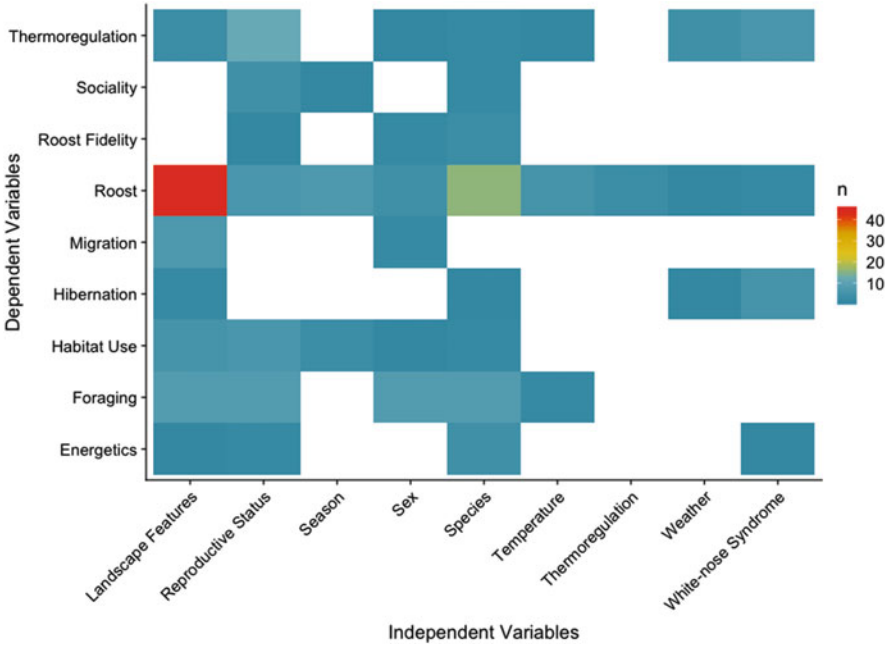

Fig. 15.6 Heat map representing the number of times a dependent and independent variable occur together in the dataset, showing combinations that have been investigated in greater than five presentations at NASBR

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

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

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

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

15.4 Looking Back and Looking Forward

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

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

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

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

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Chapter 16
Introduction and Implementation of Harp Traps Signal a New Era in Bat Research

Iroro Tanshi and Tigga Kingston

Abstract Flight and nocturnal behavior hinder direct observation of bats, limiting our knowledge of their ecology, thus creating the impetus for effective capture techniques. Mist nets have been used to trap bats for nearly a century, but are less effective under certain scenarios, including when nets are easily detected and avoided by many aerial and gleaning insectivores foraging in clutter and edge space. The invention of the harp trap gave access to these “mist net avoiders”, signaling a new era in bat research. First announced at the second North American Symposium for Bat Research (NASBR), a major modification popularized the use of harp traps among bat scientists. We conducted a global review of the literature and implemented two bibliometric analyses to reveal the contribution of harp traps to bat research. First, we show that globally, harp trap deployment is rising steeply, with the highest number of published harp trap studies reported from North America, Southeast Asia and Oceania (mostly Australia). Harp trap use is low in Central/South America, likely driven by a research emphasis on species of Phyllostomidae (readily captured in mist nets). Harp traps are rarely used in Africa except southern Africa and Madagascar. Our second bibliometric analysis focused on the impact of harp traps as a tool contributing to species discovery in Southeast Asia where it has contributed to over 50% of all species descriptions in the region by 2014. In sum, we show that the invention and implementation of harp traps has advanced our knowledge of bat taxonomy, diversity patterns, community assembly and ecology, upending dogmas and misconceptions, all with conservation implications. However, regional shortfalls in harp trap deployment is evident in Central, East and West Africa, as well as the Neotropics. Being species rich, these regions represent new frontiers for the use of harp traps that will likely lead to many discoveries.

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16.1 Introduction

The taxonomic and ecological diversity of bats has fascinated biologists for decades, but flight and their nocturnal habits limit direct observation of these animals' biology, behavior and ecological interactions. Thus, the need to capture individuals has been central to studies of bat diversity and ecology. Prior to the early twentieth century, bats were collected by hand at roosts (unfurled leaves, cave hibernacula or thatch roofs) or shot at roosts or in flight with shotguns (Vestjens and Hall 1977; Youngson and McKenzie 1977). The introduction of various forms of netting in the twentieth century (Moffat 1900; Jackson 1926; Lyman 1926; Griffin 1934), including bird nets (Allen 1938) and mist nets (Dalquest 1954), precipitated a quantum leap in our understanding of bat diversity (Bradley and Dowler 2019).

Harp traps were first described in 1958 as a method to collect large numbers of bats within a relatively short time (Constantine 1958, 1969; Constantine and Villa 1962). The trap comprised a single bank of 0.3 mm steel strings (music wires) strung vertically between rods and proved more effective at capturing *Myotis* species than mist nets. Tuttle made key modifications to the design that were shared at the second annual meeting of the North American Symposium for Bat Research (Tuttle 1971). Harp traps have thus been in use throughout most of NASBR's history, and researchers have made a range of modifications intended to improve capture success or allow deployment in different trapping scenarios. For example, capture success improved with a reduction of wire width to 0.20 mm (Tuttle 1974), an increase in the number of banks (Tuttle 1974; Francis 1989), switch to monofilament fishing line (Kunz and Anthony 1977), and offset in string position between alternating banks (Francis 1989). Traps have also been modified to allow portability (e.g., Francis 1989; Tidemann and Woodside 1978), use at tree roosts (Sedgeley and O'Donnell 1996), and even the ability to catch large pteropodids (Tidemann and Loughland 1993).

The success of different trapping techniques is strongly influenced by the habitat and trapping situation, ecology of target species, and sensorimotor systems of the bats. Echolocating bats can be classified into four foraging ensembles: (1) aerial insectivore in vegetation-free space (open space); (2) aerial insectivore in background-clutter (edge space) or at the vegetation edge; (3) aerial insectivore in highly cluttered space (forest understory); and (4) gleaning insectivore, frugivore or nectarivore (phyllostomids) in highly cluttered space (forest) (Kalko et al. 1996; Schnitzler and Kalko 2001). Each ensemble is defined by the perceptual requirements for detecting, characterizing and localizing food resources in the habitat, and thus functionally related to echolocation signal design (Schnitzler and Kalko 2001). These differences also shape which methods are most appropriate for capturing species from each ensemble.

Mist nets are primarily suited for bats foraging in open and edge spaces across the Old - and New World, as well as phyllostomids in the Neotropical forest understory. They are also effective at capturing Old World plant-visiting bats (Pteropodidae) when placed near a flowering or fruiting tree. Mist nets can be installed at ground or canopy levels, and in a variety of configurations depending on the target group (Kunz et al. 2009). However, many species are able to avoid mist nets, and this may have biased interpretation of diversity patterns across spatial and taxonomic scales and limited our understanding of the ecology and taxonomy of "mist-net avoiders" i.e. species that are difficult to capture in nets.

In contrast, although they come with their own limitations and biases (see Sect. 16.4.2), harp traps have proven successful at capturing many species of mist-net avoiders and can be deployed in situations where mist nets cannot be used or are ineffective. In this review, we assess the influence of harp traps as a research tool on field surveys, new species discoveries, taxonomic revisions, and natural history and ecological research.

16.2 Increasing Global Deployment of Harp Traps

16.2.1 Global Bibliometric Analysis of Harp Trap Deployment

To assess the extent of the use of harp traps, we conducted a bibliometric analysis of published literature. We used the Publish or Perish software (Harzing 2007) to perform a global search of the online database Google Scholar with the following terms: "Chiroptera" AND harp trap OR Tuttle trap OR Constantine trap OR "trampa arpa" (Spanish for harp trap). To avoid missing publications archived in non-text format e.g. (image formats), and those where the equipment was used but not explicitly mentioned, we also downloaded papers that cited Constantine (1958) or Tuttle (1974). Our search spanned the period since Constantine's paper in 1958 to July 12th, 2019. To perform a suitability check, we downloaded and read each publication to determine whether harp traps were used in field surveys. This approach excluded book chapters, dissertations/theses, grey literature, meta-analyses, and review articles. In addition, we extracted the following information from suitable publications: (1) additional trapping techniques used; (2) trap placement (forest or roost); (3) country of study; and (4) region. To capture broad faunal affiliations and for simplicity, we classified (with a few exceptions) regions that mostly represent the seven major land divisions/continents: Africa, Asia, Europe, North America (except Mexico), Oceania, Central/South America, and Southeast Asia. All islands around Africa were assigned to Africa. Mexico and all Caribbean islands were assigned to Central/South America. Turkey along with "Western Asia" or Arabia and Russia were included in Asia. Australia, New Zealand, Micro- and Polynesia were included in Oceania.

16.2.2 Results of Bibliometric Analysis

The bibliometric search yielded 2698 records of which 1064 met our criteria of harp trap deployment in the field (Fig. 16.1). Of these, 353 papers used only harp traps, 471 also employed mist nets, 164 added mist nets and other methods (acoustic detectors, hand capture, and butterfly/hand nets), 76 used other methods but not mist nets. There has been a rapid increase in papers reporting use of harp traps since 2000 (Fig. 16.1), which coincides with the commercial sale of harp traps by Faunatech, i.e. the release of the Austbat model in 1995 (Schulz and Hannah 1998). This suggests that the increased use of harp traps followed commercial availability of the equipment.

There are clear differences in harp trap use across regions of the world. North America had the highest publication count for each decade since the invention of harp traps until being surpassed by Southeast Asia in the current decade (Fig. 16.2). In addition, there are distinct differences in the placement and deployment of harp traps. In North America, 69% of 261 studies deployed traps at roosts. In contrast, in Southeast Asia, 74% of 189 studies placed traps in the forest understory. There are also geographic differences in how harp traps are used within regions. For example, 77% of papers reporting the use of harp traps for bat surveys in Africa occurred in southern Africa, and the Western Indian Ocean Islands, especially Madagascar. This aligns with the well-recognized dearth of local expertise in Central, East and West African countries, where only one or two countries have established local bat

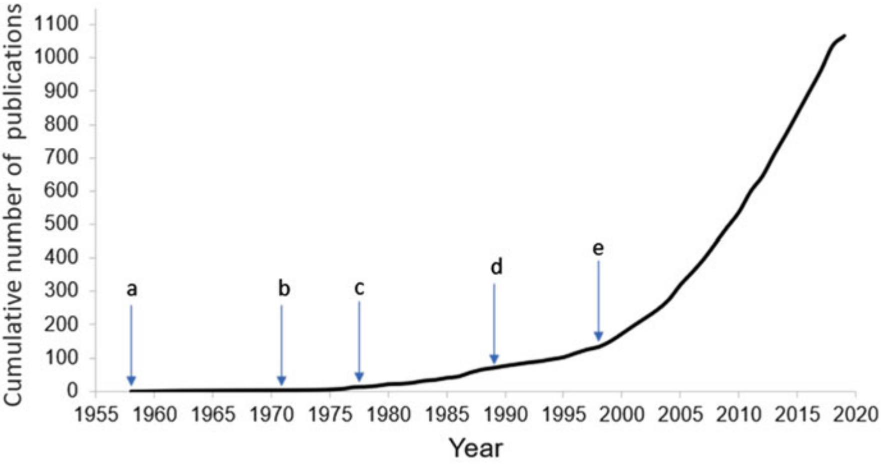

Fig. 16.1 Use of harp traps (HT) has increased over time as reported in publications. Each arrow and accompanying letter represents a major event in the development of harp trap use; (**a**) invention (Constantine 1958), (**b**) introduction to North American researchers two-bank (Tuttle 1971), (**c**) introduction to Australia (Tidemann and Woodside 1978), (**d**) four-bank design introduced to Southeast Asia (Francis, 1989) and (**e**) commercially available version—Austbat (Schulz and Hannah 1998)

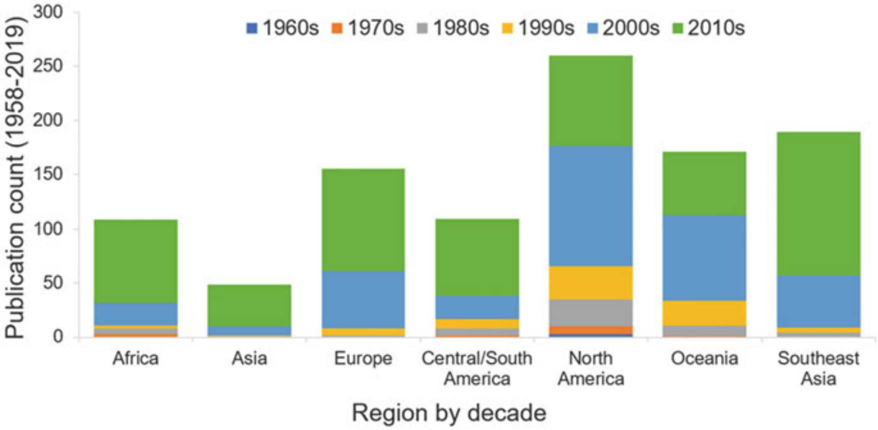

Fig. 16.2 Count of publications reporting harp trap deployment differs across region and decade. The analysis started from 1960 because only Constantine 1958's publication occurred prior to that year

biologists e.g., Burkina Faso, Cameroon, Central African Republic, Kenya, and Uganda. There has been less use of harp traps in the Neotropics (Fig. 16.2), despite the substantial research effort in the region for the past 40+ years (Kingston 2013). This is likely because of the great taxonomic and ecological diversity of the Phyllostomidae that are readily sampled using mist nets.

16.3 Consequences of Harp Traps for Bat Research

16.3.1 *Implications for Inventories and Assemblage Structure*

In many parts of the world, harp traps have improved characterization of assemblage structure of local bat faunas (Francis 1989; Fenton et al. 2001; Kingston et al. 2003). Most bat faunas include species capable of avoiding mist nets, but forest Paleotropical assemblages commonly comprise numerous species of Rhinolophidae, Hipposideridae, and the vespertilionid subfamilies Kerivoulinae and Murininae that are poorly represented in mist-net surveys but are effectively captured in four-bank harp traps (Francis 1989; Kingston et al. 2003). For example, harp traps set in a Malaysian rainforest captured 440.2 insectivorous bats per 100 trap nights compared with 7.5 individuals for a similar mist netting effort (Francis 1989). These species are aerial insectivores that rely on clutter-tolerant echolocation and maneuverable flight for foraging in highly cluttered spaces of the forest understory (Kingston et al. 1999; 2000; Senawi and Kingston 2019). Edge-space bats are also occasionally captured in harp traps in Old World forests, most commonly when traps are set near clearings (e.g., *Glauconycteris* spp., *Myotis* spp.), forest roosts (e.g., *Emballonura* spp.), over streams, or at capture stations that use mist nets to funnel bats into the traps (e.g., large-footed *Myotis* spp. foraging over rivers; Francis 1989; Kingston et al. 2003; I. Tanshi unpubl. data). Interestingly, harp traps have also been successfully used in semi-open areas in Australia, capturing predominantly vespertilionids and molossids.

Significantly, not only do harp traps capture more individuals, but they capture different species than do mist nets. Prior to the mid-1990s, Krau Wildlife Reserve in Peninsular Malaysia had been surveyed extensively with mist nets, resulting in the capture of 33 insectivorous species. Subsequent intensive use of harp traps added 15 species to the list (Kingston et al. 2003), including two previously undescribed species (later described as *Kerivoula krauensis* (Francis et al. 2007) and *Hipposideros kunzi* (Murray et al. 2018)).

Species exclusively captured in harp traps are commonly reported in multi-method studies from elsewhere in the Paleotropics (e.g., Francis 1995; Sedlock et al. 2008; Furey et al. 2010; Fahr and Kalko 2011; Patterson et al. 2017), and some species have only ever been captured in harp traps (e.g., *Kerivoula krauensis*), or rediscovered using them (e.g., *Phoniscus papuensis* which was thought to be possibly extinct in Australia before harp trap surveys (Schulz 1995)). Similarly, critically important populations of *Hipposideros curtus* were recently captured for the first time in Nigeria. This may represent the last known long-term roost of *H. curtus* following extirpation of many roost populations in Cameroon (Mickleburgh et al. 2008). The Nigerian population is now the focus of an intensive conservation program.

The ease with which phyllostomids are captured in mist nets has led to an under-appreciation of the contribution that harp traps could potentially make to diversity studies in neotropical forests. Many members of the insectivorous families, namely Mormoopidae, Emballonuridae, Vespertilionidae and Natalidae, commonly avoid mist nets but are frequently caught in harp traps (Fenton et al. 2001; MacSwiney et al. 2008; Pech-Canche et al. 2011; Herrera et al. 2018). For example, surveys of bat assemblages in Lamanai Forest, Belize reported forest understory and edge-space species captured in harp traps (Fenton et al. 2001; Herrera et al. 2018). For example, of the 32 species reported by Herrera et al. (2018) 24 were captured in harp traps and 29 in ground mist nets. Five species (*Pteronotus davyi, P. mesoamericanus, Rhogeesa aeneus, Myotis elegans,* and *M. keaysi*) were captured mostly in harp traps (Fenton et al. 2001; Herrera et al. 2018). However, the data from both studies indicate that unlike the mormoopids (*Pteronotus davyi, P. mesoamericanus*) that forage primarily in the forest understory, all other non-phyllostomids collected in harp traps are edge species. Moreover, phyllostomids were collected mostly in mist nets (Herrera et al. 2018). The tendency to capture edge-space bats in harp traps is consistent between Old and New World surveys.

16.3.2 Capture of Bats at Roost Entrances

Harp traps have also improved the ability to survey at roosts, particularly at roost entrances where large numbers of individuals are exiting simultaneously, or where it is difficult to hoist a net to cover the exit. It is often unethical to use mist nets when capture rates are high, because entanglement of many individuals makes it difficult to safely handle captured animals. Harp traps easily sample cave dwelling and tree roosting bats irrespective of foraging mode, and bats can be quickly removed from the collection bag, allowing humane capture of high numbers (Arbuthnott and Brigham 2007; Garroway and Broders 2008; Schowalter 1980). In New Zealand, harp traps have been suspended from vegetation hanging over a cave entrance (O'Donnell 2002). Harp traps at cave entrances must still be attended, as bats can quickly accumulate in collection bags, creating unsafe conditions for trapped individuals. However, capture can quickly be stopped by removing the collection bag, turning the trap parallel to the flow of bat traffic, or moving it completely out of the flight path.

16.3.3 New Species Descriptions

Many new species descriptions are based on first-time captures or higher number of individuals collected in harp traps, particularly in Southeast Asia, where at least 48 species have been described in the last 15 years (Bates et al. 2004; Bates et al. 2007a; Csorba et al. 2007; Bates et al. 2007b; Francis et al. 2007; Kruskop and Eger 2008; Furey et al. 2009; Thong et al. 2012; Soisook et al. 2013; Son et al. 2015). To quantify the relative contribution of harp traps to the description of new species, we reviewed the literature to determine the proportion of new species descriptions based on bats captured in harp traps relative to mist nets since 1984 and the last description prior to 1989 when harp traps were first deployed in Southeast Asia. We conducted a bibliometric search using the following search terms in Google Scholar: "sp. nov" AND "chiroptera" and each of the 11 countries in the region. We also searched a global database of bat species descriptions (Paul Bates, unpubl. data). We aggregated and downloaded the results of the Google Scholar search (list of publications) using the Publish or Perish software (Harzing 2007). We report relative contributions of harp traps versus mist nets on total bat descriptions in the region (Fig. 16.3a) and forest-dependent understory bats belonging to the families Rhinolophidae, Hipposideridae, and subfamilies Kerivoulinae and Murininae, that forage primarily in the forest understory.

Following the suggestions for modification and deployment of harp traps by Francis (1989), we show that nets and harp traps contributed more or less equally to overall increase in species descriptions (Fig. 16.3a), but harp traps are particularly important for description of understory bats (Fig. 16.3b). Although it appears that the role of harp traps in species descriptions started gradually, this initial lag may be due

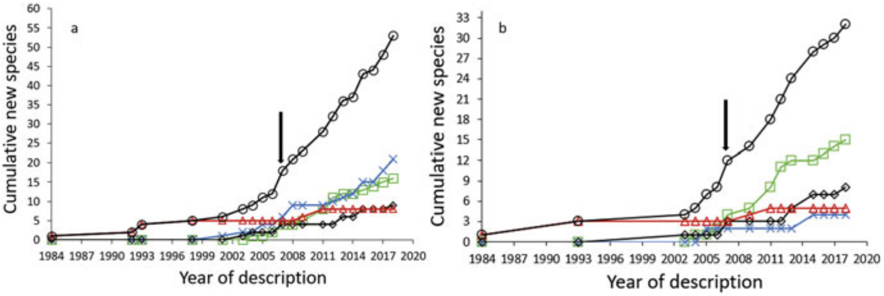

Fig. 16.3 Accumulation curves of new bat species descriptions from Southeast Asia (SEA) (1984–2019). (**a**) All bat species described and (**b**) forest dependent understory species. Symbols represent species descriptions based on captures in harp trap only (green hollow squares), mist net only (blue cross), harp trap and mist net (black hollow diamonds), unreported trap type (red hollow triangles) and total across trap types (black hollow circles). Arrows indicate the launch of SEABRCU in 2007

to the need to accumulate and examine materials collected, and constraints on in-region taxonomic expertise. For example, following Francis (1989), the first new species described (Robinson et al. 2003) was based on a harp trap capture made in 1993. Furthermore, the leap in new species descriptions coincides with the launch of Southeast Asian Bat Conservation Research Unit (SEABCRU) in 2007 (Kingston 2010). One of the research priorities of the SEABCRU during that period was the conservation of forest-dependent bats, and the group worked to promote harp trap surveys of bats in unmodified forests. Thus, intense field surveys that employed harp traps has allowed discovery of new species that would be otherwise difficult or impossible with only mist nets. A second SEABCRU priority focused on development and networking of regional taxonomic expertise, that has greatly improved capacity to undertake species descriptions. Subsequent support of SEABCRU as a Research Coordination Network by the National Science Foundation, USA in 2011 allowed for even more intense efforts, but it was noted at a workshop in Thailand in 2012 that harp traps were already widely used across the region, and being easily reproduced using readily available local materials (TK pers. obs.). This coincides with the fact that by 2007, exclusive harp trap captures contributed >30% to all new species description and 50% of forest understory bats, and up to 70% where both harp traps and mist nets were deployed by 2013 (Fig. 16.3).

Similarly, accumulation of new museum material (specimens) as a direct result of a series of harp trap captures has paved the way for taxonomic resolution and revision of species complexes and cryptic species (Francis et al. 2007; Furey et al. 2009; Kruskop and Eger 2008; Soisook et al. 2013; Son et al. 2015; Murray et al. 2018). Together, this corroborates reports that spatial and temporal bias in bat species distribution patterns across Southeast Asia is linked to methodological invention, in this case the harp trap, driving knowledge of species distribution patterns (Fisher-Phelps et al. 2017).

By uncovering species new to science, and previously unknown diversity patterns and ecology (see Sect. 16.3.4), the harp trap as a methodological innovation has implications for species conservation. Confusion about species taxonomy has consequences for species conservation (Tsang et al. 2016), but taxonomic resolution often requires access to multiple individuals of the species and harp traps facilitate this for the species that avoid mist nets. Given their success in Southeast Asia, we anticipate that greater deployment of harp traps in Africa and the Neotropics will uncover new species, and increase regional and country records, enabling bat conservationists to identify at-risk species and design and implement conservation programs.

New species discoveries, and more complete knowledge of local assemblage compositions have led to the revision of national and regional species checklists (Huang et al. 2014; Soisook 2011). This improves our knowledge of regional and global patterns of bat diversity. Previous sampling efforts, based primarily on mist nets, led to the conclusion that Paleotropical communities were depauperate relative to Neotropical ones (Findley 1993). The collection of 72 bat species from a single site in Malaysia, 22 of which were captured exclusively in harp traps (Kingston et al. 2003; 2006) is comparable to high diversity sites with similar size (3 m^2) such as Paracou in the Neotropics, where 78 species are known (Simmons and Voss 1998). Subsequent surveys support the finding that many Paleotropical assemblages are species rich (e.g., Sumatra—Huang et al. 2014). Similarly, recent surveys using harp traps in unmodified rainforest in Nigeria have found species richness comparable to many sites in Southeast Asia (I. Tanshi, unpubl. data), suggesting that supposed depauperate bat diversity in tropical Africa may also be a sampling artifact.

16.3.4 Consequences for Ecological Studies

Beyond understanding bat assemblage structure in intact forests, fragmentation of natural areas raises questions about how species-rich assemblages may be disassembled. For example, surveys with harp traps in a forest landscape fragmented by oil palm and rubber plantations demonstrated that not only does bat species richness decline in fragments, but so too does the genetic diversity of insectivorous species that roost and forage in forests (Struebig et al. 2011). A complementary trapping program—one that used mist nets, harp traps and tunnel traps in agro-pastoral habitats in the Philippines found that plantations adjacent to forest can provide roosting opportunities, contradicting previous studies (Sedlock et al. 2008). Similarly, in the Neotropics, phyllostomids and non-phyllostomids respond negatively to vegetation loss (Clarke et al. 2005; Williams-Guillen and Perfecto 2011). Not surprisingly, complementary sampling that included harp traps in Mexico demonstrated that bat activity decreased along a gradient of agricultural intensification from forest to intensely managed coffee plantation. However, the use of harp traps highlighted that, unlike open space bats, aerial insectivores in cluttered and edge space were more sensitive to the intensification gradient (Williams-Guillen and Perfecto 2011).

In addition to advancing knowledge about taxonomy and local and regional diversity patterns, harp traps have significantly impacted knowledge accumulation about bat ecology. In part, this is because information can be gathered from a bat in the hand (Kunz et al. 2009), such as sex and reproductive condition that provide information about reproductive patterns (Laval and Laval 1977; Kunz 1974; Furey et al. 2011; Nurul-Ain et al. 2017), or samples taken from a captured bat, such as wing tissue for genetic studies (e.g. Rivers et al. 2005, Senior et al. 2005; Rossiter et al. 2012), feces to explore dietary and foraging ecology (Anthony and Kunz 1977; Schulz and Wainer 1997; Whitaker Jr et al. 2004) and more recently, microbiome composition (Phillips et al. 2012; Carrillo-Araujo et al. 2015; Dietrich et al. 2017; Phillips et al. 2017). Insights into echolocation signal design and function can be gathered from recordings and behavioral experiments using captured bats (e.g., Schmieder et al. 2012). Also, telemetry devices attached to captured bats open the window for studies on roosting and movement ecology (Sedgeley and O'Donnell 1996; Schulz 1995).

16.4 Discussion and Conclusion

In this review, we have provided evidence that surveys using harp traps have facilitated new species discoveries, taxonomic revisions and cryptic species resolution, leading to new locality records, and revision of national and regional checklists. The use of harp traps has also allowed for investigations into bat biology, ecology and behavior, challenging misconceptions for previously unexamined or under-sampled groups, while contributing to the general ecological discourse.

16.4.1 Reduced Stress to Captured Bats

Mist nets entangle and largely immobilize captured bats. This is presumed to be stressful for the bats, so it is recommended that nets be checked every 10–15 min (Sikes et al. 2016), and many researchers prefer to remain close to open nets. Moreover, substantial training and practice is required to enhance rapid extraction times from mist nets that minimize stress. In contrast, bats captured by harp traps are held in a collection bag that allows some movement and the ability to hang from the sides of the bag, and individuals commonly roost under the plastic flap that prevents them from climbing out. Although this has not been evaluated directly, this is likely less stressful than mist net entanglement, and certainly allows for easier retrieval of captured individuals (Fukui et al. 2001; Kingston 2016).

16.4.2 Limitations of Harp Traps

Despite the utility of harp traps, they typically require: (1) closed habitats in which the vegetation funnels bats into the trap, or (2) a common flight path (Fig. 16.4a), or (3) a roost exit (cave entrance or tree roost) that can be surveyed (Fig. 16.4b). As might be expected, harp traps deployed across a gradient of tree cover (forest block, dense scattered trees, moderate scattered and sparse scattered) yielded bat abundance and diversity directly correlated with tree density in Australia (Lumsden and Bennett 2005) (Fig. 16.4c). Notwithstanding, harp traps have also captured bats in sparse vegetation in Australia. For instance, the first record of a *Mormopterus* sp. in Australia came from a harp trap set under a single eucalyptus tree in open habitat (Ellis 2001), and one trap placed between three trees surrounded by a grassy landscape caught 29 individuals of seven species (Lumsden and Bennett 2000). Generally, harp traps are less effective in more open habitats such as uncluttered urban (Hourigan et al. 2009) and savanna areas.

Even when deployed in suitable habitat, Berry et al. (2004) reported that only 4% of individual bats that encountered traps were caught. Capture success can be improved by blocking off gaps between trap and vegetation (forest) or cave wall by using dead branches and palm fronds or plastic sheets (Winifred Frick, pers. comm. 2019; Fig 16.1b). But amazingly, some bats can still fly through a four-bank

Fig. 16.4 Photos of harp traps in different trapping scenarios. (**a**) Flight path along a forest trail in Kenya (four-bank, credits: TK), (**b**) Sampling cave roost entrance (two-bank, credits: Winifred Frick), and (**c**) Under a single tree in Australia (two-bank, credits: Lindy Lumsden)

harp trap. Although we know of no test of the effectiveness of harp traps elevated to canopy height, their use in the canopy may prove illuminating, considering how canopy nets significantly changed perceptions of bat assemblage composition in the Neotropics (Simmons and Voss 1998).

16.4.3 Future Directions

Differences in reported species richness between the Afrotropics and the Neotropics has been attributed to limited sampling across most African countries compared to an explosion in bat interests and higher survey efforts in both the Neotropics and, more recently, Southeast Asia (Paul Bates, pers. comm.). Therefore, we predict that research on bats in sub-Saharan Africa will benefit from surveys that include harp traps in the forest understory (Kingston et al. 2003; Fahr and Kalko 2011). Similarly, Neotropical surveys would likely benefit from greater use of harp traps, although none of the Paleotropical taxa (Rhinolophidae, Hipposideridae, Kerivoulinae and Murininae) are present, deployment of traps should give better coverage of frequently caught groups (Mormoopidae, Emballonuridae, Vespertilionidae and Natalidae). The use of harp traps in the canopy across all regions may reveal unexpected results.

Although while we know that harp traps are more effective than mist nets for capturing particular taxa, it is not clear why. To avoid capture, bats must first detect and then be able to avoid the net or trap. Logic suggests roles for differences in target strength of mist nets vs. harp traps, and in the echolocation call structure and maneuverability of the bats. There is some support for the significance of target strength and interactions with echolocation frequency (Berry et al. 2004), but further work is needed. Research into this would be profitable, as it could both generate insight into sensory and sensorimotor capabilities of bats, and potentially lead to even more effective trap designs.

16.4.4 Conclusion

The invention, modification and deployment of the harp trap has changed misconceptions about the global distribution of bat species richness and accelerated species descriptions and taxonomic resolutions, especially for forest understory bats in Southeast Asia. However, except for southern Africa and a few reports from Liberia, Guinea, Cote d'Ivoire, Kenya and Uganda it is noteworthy that sub-Saharan Africa remains a void in the deployment of harp traps for bat surveys, primarily due to limited local capacity. The impact of harp traps is well-illustrated by the successive waves of advances in bat research that have followed the modification and introduction of traps to Southeast Asia, where they precipitated a golden "age of discovery" (*sensu* Tsang et al. 2016) of new bat species, taxonomic revisions, species biology and key aspects of bat ecology. However, we advocate complementary trapping methods for surveys on local species assemblages (Meyer et al. 2011), except for studies that focus on a single ecological group of bats (Kingston 2016).

In conclusion, we demonstrate the pivotal role harp traps have played in the advancement of bat research. We show that leaps in global harp trap use were driven by significant modifications, introductions into new regions, commercialization, and innovative deployment. We note regional differences in harp trap deployment in roost versus forest understory and identify gaps in Africa and the Neotropics. Overall, we show that, like mist nets earlier on (Bradley and Dowler 2019), harp traps have revolutionized the study of bats over the last six decades, upending dogmas, challenging misconceptions and greatly expanding our knowledge of the incredible diversity of bats on a global scale.

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Part VIII
Molecular Systematics

Burton K. Lim

Taxonomy and systematics have long been areas of study in biology starting with the adoption of the binomial nomenclature system of Linnaeus in 1758 for animals and followed by the theory of evolution by natural selection proposed by Darwin in 1859. Morphology has been the traditional character set used, but by the first decade of NASBR in the 1970s molecular methods were becoming more prominent.

Sessions on systematics in the initial symposiums of the Society had several talks on multivariate analyses, also known then as numerical taxonomy or phenetics, and also chromosomal studies. Presentations on molecular systematics at NASBR first appeared in 1973 with a paper about bat phylogeny based on biochemical methods comparing albumin and transferrin immunology by Vince Sarich, who pioneered these techniques first on human and then mammal evolution. The chapter by Diana Moreno and Jorge Ortega outline this history of molecular biology in bat research over the past half century. Other early methods included protein electrophoresis, DNA hybridization, and restriction enzyme sites. Eventually, the direct sequencing of DNA was possible beginning with mitochondrial genes such as cytochrome b and nuclear loci. Some of the more prominent higher-level taxonomic debates involving Chiroptera were resolved with the help of molecular data, including the bat monophyly and microbat diphyly issues. Today, genomic approaches are just starting to be common and will undoubtedly drive molecular systematics into the next 50 years of NASBR.

The second chapter in this section is a review of bat phylogeography by Giovanni Hernández-Canchola and colleagues. This is a specific area of molecular systematic study and the term was coined by John Avise in 1987. In general, the chapter evaluates the geographic distribution of genetic lineages to explain the evolution of species. Recent phylogeographic studies have been applied to ecological aspects

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and conservation genetics related to taxa and habitats that require more research. Many early studies were done on mammals using mitochondrial DNA, but publications on bats did not appear until the 1990s. Although tropical regions have higher species diversity, more phylogeographic studies have been done with Palearctic species. Most publications are on Vespertilionidae, with almost twice as many as the next family Phyllostomidae. There are clearly some areas and groups in need of more research on phylogeography as NASBR enters into its second half century.

Chapter 17
Molecular Biology in the Evolution of Bats: A Historical Perspective

Diana D. Moreno-Santillán and Jorge Ortega

Abstract The North American Society for Bat Research (NASBR) was born in 1970 with the first Symposium on Bat Research, with 42 attendees and 26 presentations in Tucson, Arizona. The topics discussed in the earlier NASBR meetings were focused mostly on behavior, ecology, physiology, and taxonomy. It was not until the fourth annual symposium that Dr. Vincent M. Sarich presented the first talk on the use of molecular biology to infer phylogeny in bats. During the last 50 years, this subject has expanded rapidly with innovative techniques. Nowadays, it is widely used to understand the evolution of bat species. In this chapter, we discuss how molecular biology has contributed to bat systematics and evolutionary biology from immunological assays performed by Sarich to the use of Sanger sequencing and next generation sequencing that has allowed the assembly of whole genomes, transcriptomes, and viromes. We provide a chronology of how research in molecular biology has gained importance in the study of bat biology from one single presentation in 1973 to whole sessions in more recent NASBR meetings.

Keywords Evolutionary biology · Molecular biology · Next generation sequencing · Sanger sequencing · Vincent Sarich

17.1 Introduction

Before the development of molecular markers to infer evolutionary divergence between species, researchers used phenotypic characters (morphological and physiological) to resolve the evolutionary history of many organisms. The integration of

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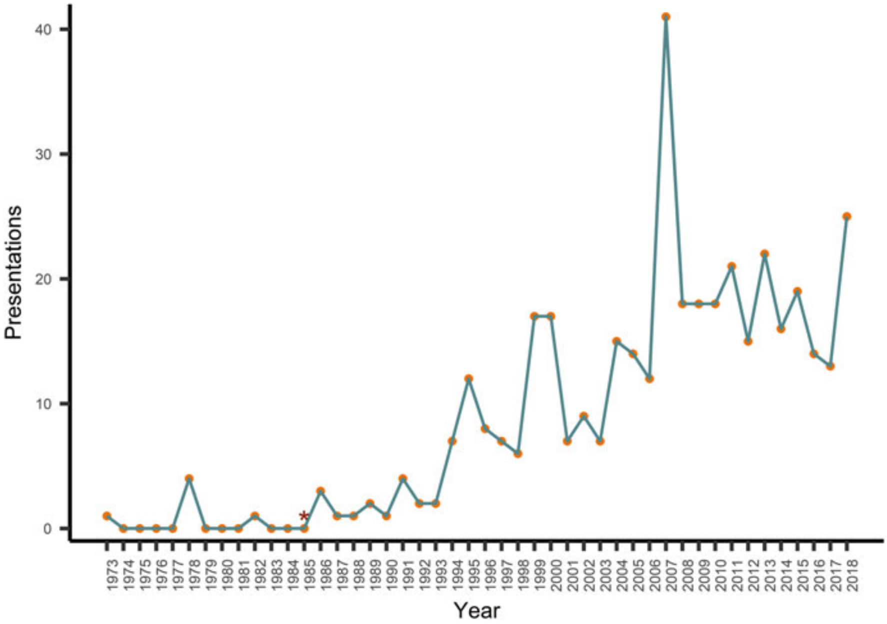

Fig. 17.1 Number of presentations that included the implementation of molecular biology techniques throughout 50 years of the North American Society for Bat Research. Data were obtained according to the content of key words in the abstract and/or title. *1985 had no NASBR meeting

molecular markers with systematics and taxonomy helps us to distinguish homologous characters (traits derived from a common ancestor) from analogous characters (convergent traits with a different evolutionary history), thus avoiding misclassifications due to parallel or convergent evolution (Avise 1994). Another advantage in the use of molecular markers is that it allows comparisons of macromolecules such as nucleic acids, enzymes, or proteins shared between species that might not share obvious morphological characters to solve taxonomic conflicts caused by homoplasy (Avise 1994; Dávalos et al. 2014).

Dr. Vincent M. Sarich (1934–2012), a professor of Anthropology at the University of California Berkeley, was one of the pioneers in determining the evolutionary relationships between species based on immunological comparisons of amino acid composition of blood proteins (albumin and transferrin). During the fourth annual symposium of the North American Society for Bat Research (NASBR) in 1973 that took place in New Orleans, Sarich gave a presentation entitled: “A molecular approach to chiropteran phylogeny: albumin and transferrin evolution in bats” during a session on taxonomy and systematics. In the short history of NASBR, this was the first talk mentioning the use of molecular markers to understand the phylogeny and evolution of bats. Sarich laid the first stone at NASBR for molecular biology, and since then this field of study has grown from one talk in 1973 to more than 20 presentations in the 49th meeting (Fig. 17.1). In addition, research has progressed from proteins to genes to genomes and transcriptomes. In this chapter, we give a historical review of the impacts of molecular biology in the study of bats encompassing systematics, immunogenetics, and evolutionary biology.

17.1.1 Biochemical Methods

Prior to the sequencing era, during the mid-1960s, the use of protein assays such as allozyme electrophoresis and immunology methods were applied to estimate genetic variability and to determine evolutionary relationships between species (reviewed by Avise 1994). Protein immunology assays using molecular markers such as albumin and transferrin proteins were developed to quantify immunological distances through antigenic cross-reactions (Sarich 1972, 1976). Albumins were purified by polyacrylamide gel electrophoresis from the species of interest; once purified, albumins from reference species were injected into rabbits to generate antiserum that contained specific antibodies for the foreign proteins. Thereafter, albumins of the query species were extracted and tested against the specific antibodies of the reference species. Finally, the amount of bound complement between the species was measured. The difference between antigen-antibody reactions was expressed as immunological distance (ID unit), with each ID unit being equivalent to one amino acid substitution (Prager and Wilson 1971).

Immunological distance was later criticized due to its reliance on overall similarity measures as opposed to evolutionary relationships because primitive traits could not be differentiated from derived forms (Wetterer et al. 2000). Despite this criticism, the technique needs to be highlighted as it formed the basis for current molecular systematic analyses.

During the mid-1960s and 1970s, studies of albumin evolution were widely used in mammals such as humans, other primates, pinnipeds, rodents, ursids, and bats (Sarich 1972). Sarich was also the first to use albumin as a molecular clock to assess primate evolution, and proposed that the time of divergence between humans and other African apes occurred five million years ago (mya) instead of −25 mya as morphological data suggested (Sarich 1972; Wilson 1985). He expanded these techniques to the field of bat systematics and published several papers with collaborators, such as Robert Baker and Rodney Honeycutt, which were mainly focused on obtaining more robust evidence of the evolutionary relationships within the diverse family Phyllostomidae (Baker et al. 1981; Honeycutt et al. 1981; Honeycutt and Sarich 1987a, b). For example, morphological data based on anatomical and dental characteristics classified the subfamily Brachyphyllinae as the sister taxon of Glossophaginae (Baker et al. 1981), whereas chromosomal data did not show evidence of such separation as both taxa had the same karyotypes (Baker and Bass 1979). In order to make a more integrative analysis, Baker et al. (1981) incorporated markers such as isozymes and albumin. Antisera from albumins of four species (*Brachyphylla cavernarum*, *Phyllonycteris aphylla*, *Monophyllus plethodon*, and *Glossophaga soricina*) were prepared in rabbits. Electrophoretic and immunological

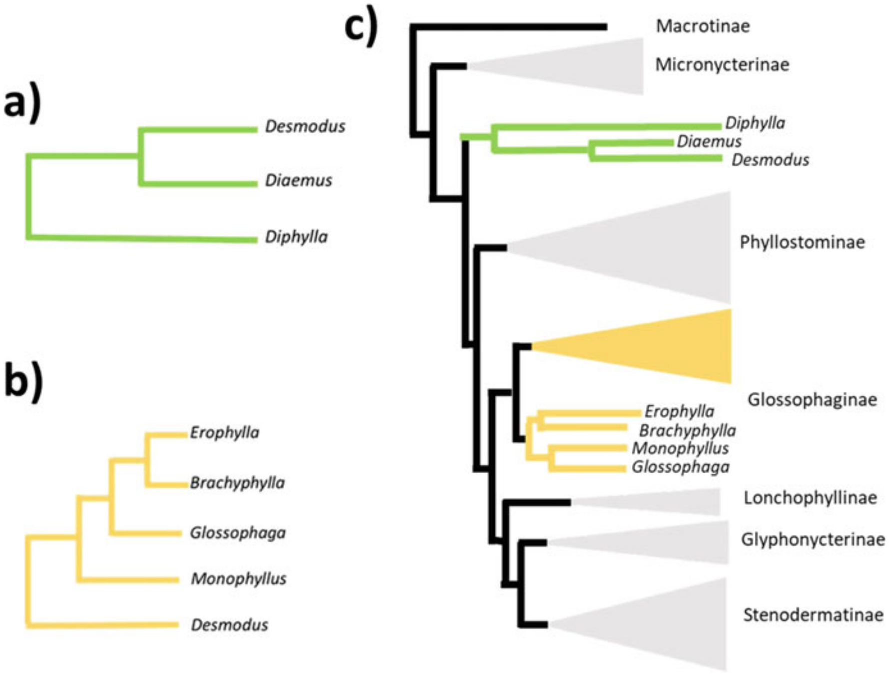

Fig. 17.2 Phyllostomid phylogenies reconstructed with analyses of molecular data. (**a**) Evolutionary relationships among the three blood-feeding bat species obtained with albumin assays (Honeycutt et al. 1981); (**b**) Evolutionary relationships within Glossophaginae obtained with albumin assays (Baker et al. 1981); and (**c**) Most recent phyllostomid phylogeny obtained with nuclear and mitochondrial genes (modified from Baker et al. 2003)

analyses confirmed the hypothesis suggested by morphological data by grouping *Phyllonycteris*, *Erophylla*, and *Brachyphylla* into a monophyletic group corresponding to the Brachyphyllinae subfamily. With these molecular markers, they also found that the molecular distance from *Phyllonycteris* to *Erophylla* was shorter than to *Brachyphylla*, and these results were consistent with morphological data. Based on the immunological assays, they suggested an alternative classification that Brachyphyllinae represents a radiation within Glossophaginae rather than a sister taxon (Fig. 17.2b—Baker et al. 1981). Evolutionary relationships among Brachyphyllinae species and with Glossophaginae suggested by electrophoretic distances were later corroborated using nuclear and mitochondrial DNA sequence data in Bayesian and maximum likelihood phylogenetic analyses, finding that *Brachyphylla* is closely related to other nectar-feeders (Dávalos et al. 2014; Baker et al. 2016). Current classification ranks Brachyphyllini and Glossophagini as 2 of 3 tribes within the subfamily Glossophaginae (Baker et al. 2016).

Allozyme electrophoresis and albumin immunology were also used to study the evolutionary relationships among the three blood-feeding bat species within Phyllostomidae: *Desmodus rotundus*, *Diphylla ecaudata*, and *Diaemus youngii*

(Honeycutt et al. 1981). Preliminary results were presented in 1978 during the ninth NASBR meeting in Albuquerque where the first session dedicated to genetics appeared. Similar to Brachyphyllini and Glossophagini, previous morphological and karyotype data yielded conflicting results regarding vampire bat classification. Morphological data had vampire bats as a monophyletic clade, where *Desmodus* and *Diaemus* formed a separate clade from *Diphylla,* whereas chromosomal results suggested that *Desmodus* was more closely related to *Diphylla* than to *Diaemus.* Allozyme and albumin molecular analyses supported the morphological classification (Fig. 17.2a). Based on the molecular clock that Sarich implemented according to the units of difference in albumin, it was estimated that *Diphylla* separated from the clade comprising *Desmodus* and *Diaemus* approximately 5–8 mya (Honeycutt et al. 1981). Evolutionary relationships of vampire bats inferred by immunological distance and electrophoretic analysis were corroborated two decades later by an exhaustive parsimony analysis including 150 characters (morphology, sex chromosomes, and restriction sites of mitochondrial DNA; Wetterer et al. 2000), and by several studies using DNA sequencing of nuclear and mitochondrial genes (Van Den Bussche and Baker 1993; Porter and Baker 2004; Hoofer and Baker 2006). However, Bayesian and maximum parsimony phylogenies (Baker et al. 2003; Dávalos et al. 2014; Baker et al. 2016) refute the placement of Desmodontinae as the basal branch of phyllostomids, as suggested by albumin immunological distance (Honeycutt et al. 1981; Honeycutt and Sarich 1987a). Instead, these DNA-based analyses supported Macrotinae as the basal branch of Phyllostomidae, followed by Micronycterinae and Desmodontinae (Fig. 17.2c; Baker et al. 2003).

In 1982, immunological and electrophoretic techniques were used in an integrative analysis with morphology and karyology to resolve the phylogeny of three families of bats (Noctilionidae, Mormoopidae, and Phyllostomidae), and to test the existence of the Phyllostomoidea superfamily (Arnold et al. 1982). Some authors associated *Noctilio* with the family Emballonuridae, whereas karyological studies considered that it was more closely related to mormoopids and phyllostomids (Patton and Baker 1978). By analyzing the datasets individually, Arnold et al. (1982) did not find congruence between the phylogenies, due to several limitations such as the use of insufficient morphological characters, the inability of electrophoretic assays to resolve synapomorphic states between mormoopids and noctilionids, and the lack of chromosomal homologies to make conclusive comparisons. However, an integrative analysis of these datasets proposed a phylogenetic tree that supported the hypothesis of a Phyllostomidae-Noctilionidae-Mormoopidae superfamily.

Based on another study of albumin distances of 22 species, it was proposed that phyllostomid diversification occurred faster in at least three extant lineages and that Phyllostominae was a paraphyletic clade in relation to other subfamilies including *Lonchorhina*, *Macrophyllum*, *Mimon*, *Trachops*, and *Chrotopterus* (Honeycutt and Sarich 1987a, b). Afterwards, with the implementation of DNA sequencing of nuclear and mitochondrial genes, a new evolutionary relationship was proposed, where *Lonchorhina, Macrophyllum*, and *Mimon* form an independent monophyletic clade corresponding to a new subfamily: Lonchorhininae (Baker et al. 2003; Dávalos et al. 2014; Baker et al. 2016).

17.1.2 DNA–DNA Hybridization

The molecular DNA-DNA hybridization technique measures the degree of similarity between two species based on the melting temperatures required to dissociate hybridized strands of DNA. This technique was presented in the NASBR 1992 meeting by William Kilpatrick and Pedro Nuñez, where they supported bat monophyly during the bat diphyly debate that suggested a closer relationship of Old World fruit bats (Pteropodidae) to primates than to laryngeal echolocating bats based on visual pathways (Pettigrew 1986). Although Kilpatrick and Nuñez never published their results, another DNA-DNA hybridization study showed that bats from different suborders were more closely related to each other than to other eutherian species (Kirsch et al. 1995). The microbat diphyly debate was also instigated by this molecular technique. Using single-copy DNA hybridization, Rhinolophoidea formed a monophyletic group with Pteropodidae and not with the other laryngeal echolocating microbats (Hutcheon et al. 1998). These results were previously presented by the authors during the 1995 NASBR meeting. Microbat paraphyly was later corroborated by nuclear sequence data (Teeling et al. 2005). Although these higher-level relationships of bats were supported by DNA-DNA hybridization, this molecular technique was based on overall genetic similarity and not on shared derived characters amenable to tracking evolutionary change.

17.1.3 Gene Sequencing

Sanger sequencing, also known as the chain termination method, was developed by Sanger et al. (1977), in an effort to determine the nucleotide arrangement of small DNA fragments. But it was not until 1986, when the first-generation automated sequencers appeared, that fluorescence-based Sanger sequencing increased exponentially. This was followed closely by the Polymerase Chain Reaction (PCR), which enabled the amplification of targeted genes.

Mitochondrial DNA was targeted in early molecular systematic studies because of its multiple identical copies in a cell, as opposed to a single biallelic nucleus. The cytochrome-b gene (*cytb*) has been widely sequenced in mammals by virtue of its high mutation rate, which facilitates the analysis of evolutionary relationships at the intrageneric and intraspecific level. As a contrast to the maternal inheritance of the mitochondrion, nuclear genes, such as the more slowly evolving RAG2 (Recombination-Activating Gene-2) exon, have been sequenced to study the systematics of several families of bats. For example, *RAG2* and *cytb* have been sequenced for Phyllostomidae (Van Den Bussche and Baker 1993; Baker et al.

2000; Porter and Baker 2004; Hoofer and Baker 2006), Pteropodidae (Goodman et al. 2010; Almeida et al. 2011; Cunha et al. 2016), Mormoopidae (Lewis et al. 2001), and Vespertilionidae (Ruedi and Mayer 2001, Kawai et al. 2003; Bickham et al. 2004; Larsen et al. 2012).

Gene sequencing has been a useful tool for cryptic species identification, such as in the *Myotis* genus. By analyzing *cytb* from 215 specimens, Larsen et al. (2012) were able to identify a greater proportion of species richness in South America than expected, contradicting the hypothesis that North American lineages were more diverse than southern lineages. The authors suggested that clades diversified more rapidly in southern than in northern species as a consequence of a greater diversity of potential ecological niches allowing specialization.

Another important application of mitochondrial genes has been the study of migration patterns and population genetics. Studies using mitochondrial *cytb* and nicotinamide adenine dinucleotide dehydrogenase subunit I (*ND1*) sequences demonstrated that the biogeographic distribution of species predicts the phylogeny of *Myotis* species better than morphologic data. Despite the broad morphological diversity that this group possess, genetic data grouped all New World species in a well-supported monophyletic clade. However, *cytb* and *ND1* also placed *M. brandtii,* a European vespertilionid, in the New World clade, which suggests colonization of Eurasia through the Beringia land bridge from North America (Ruedi and Mayer 2001; Kawai et al. 2003; Bickham et al. 2004).

Hebert et al. (2003) proposed the use of the mitochondrial cytochrome c oxidase I (COI) as a barcode gene for species identification of all animals. The effectiveness of COI in bat identification was tested with success in Neotropical bats (Clare et al. 2007). Consequently, the barcoding technique has been widely used since then to estimate biodiversity and genetic variation in Chiroptera (Hernandez et al. 2012; Lim and Arcila 2015; Chaverri et al. 2016; Loureiro et al. 2018; Pavan et al. 2018).

One of the most important contributions to bat systematics by molecular biology in the twenty-first century was the recognition of the Yinpterochiroptera and Yangochiroptera suborders (Springer et al. 2001; Teeling et al. 2002). Nuclear genes showed that the Megadermatidae, Craseonycteridae, Rhinolophidae, and Rhinopomatidae families, formerly classified within Microchiroptera, were more closely related to the Megachiroptera (family Pteropodidae) than to the other echolocating bats Teeling et al. 2005). Part of this research was presented in 2003 during the 33rd symposium in Lincoln, Nebraska. The same evolutionary relationships have been supported by subsequent phylogenetic analyses of orthologous genes obtained by genomic and transcriptomic analyses (Lei and Dong 2016; Hawkins et al. 2019; Moreno et al. 2019).

17.1.4 Genomics and Transcriptomics

Molecular biology in bat research has increased over the past half century, progressing from biochemical studies such as protein electrophoresis and immunological assays to DNA sequencing by Sanger methods to recover individual genes to next generation sequencing technology (NGS) to assemble whole genomes/transcriptomes. Bats have small genomes (approximately 2Gb) compared to other mammals, but have many unique evolutionary adaptations that allowed the evolution and radiation of the second-most species-rich mammalian order. Genome and transcriptome analyses give us a wider comprehension of these adaptations, such as flight, echolocation, longevity, and immunity (Teeling 2009; Shen et al. 2010; Dong et al. 2013; Zhang et al. 2013; Foley et al. 2018).

17.1.4.1 Evolution of Flight

A comparative high-throughput genome study between *Pteropus alecto* and *Myotis davidii* revealed insights into candidate genes related to the origin of flight in Chiroptera (Zhang et al. 2013). Most of these genes are involved in DNA damage checkpoint and repair, suggesting that strong positive selection on these genes acts to mitigate the collateral damage of oxidative metabolism resulting from the high metabolic rates required for flight. This change in metabolic energy seems to be the key to comprehending the origin of flight in these mammals. Coding genes for the mitochondrial respiratory chain (oxidative phosphorylation genes, OXPHOS) were analyzed by Shen et al. (2010), as this pathway produces 95% of ATPs required for locomotion. OXPHOS genes formed a monophyletic clade for bats, suggesting a single origin of flight in the Chiroptera lineage. Applying a maximum likelihood approach, 4.9% of the mitochondrial and nuclear genes were found to be under positive selection in Chiroptera, with cytonuclear coevolutionary constraint occurring among these genes during the evolution of flight.

17.1.4.2 The Genomics of Echolocation

The evolutionary origin of laryngeal echolocation was thought to be a synapomorphy that appeared once in the lineage formerly known as Microchiroptera, with one family (Pteropodidae) formerly known as Megachiroptera lacking this adaptation. However, recent evidence based on molecular data suggested that some of the echolocating microbats are more closely related to Pteropodidae than to the other echolocating species (Teeling et al. 2005). This new classification leads to two new competing hypotheses about the evolutionary origin of echolocation: (1) a single origin of laryngeal echolocation that was lost in the pteropodid lineage; and (2) two independent gains of echolocation in the Chiroptera radiation (Eick et al. 2005; Teeling 2009). Molecular analysis seems to support the second hypothesis, showing convergent evolution in genes involved in hearing and vocalization (Teeling 2009; Parker et al. 2013). Whole genome sequencing suggests that there are at least seven genes related to echolocation (*SLC26A5, MMP14, DZIP1, TMC1, FOXP2, FOS,* and *WNT8A*) that are under positive selection in echolocating bats (Zhang et al. 2013). However, a recent study of cochlear development in the inner ear suggests a single origin of echolocation in bats (Wang et al. 2017). This is supported by comparative anatomy and the suggestion that the most recent common ancestor of bats had the ability to echolocate (Thiagavel et al. 2018; Arbour et al. 2019).

There are two principal genes of interest to understand bat echolocation: the vocalization gene *FOXP2* and the hearing gene *Prestin. FOXP2* is a transcription factor involved in vocalization in mammals, which is highly conserved in this group. In bats, however, *FOXP2* is extremely variable and shows evidence of being under positive selection (Teeling 2009; Zhang et al. 2013). *Prestin*, also known as *SLC26A5,* encodes a transmembrane protein that allows amplification of cochlear sensitivity in mammals. In echolocating bats, this gene has rapid evolutionary rates (Teeling 2009; Seim et al. 2013; Zhang et al. 2013).

Transcriptomic data generated by *de novo assembly* also contributed to the understanding of echolocation. A comparative study of inner ear transcriptomes between the echolocating *Myotis ricketti* and the non-echolocating *Cynopterus sphinx* revealed up-regulated genes in *Myotis* that are involved in morphogenesis of the cochlea, which is a specialized structure in bats for high frequency sounds and sound sensory perception (Dong et al. 2013). These characters are also differentiated by morphological analysis, where the cochlear apparatus is larger in echolocating species. Both genomic and transcriptomic data indicate that the *TMC1* gene, encoding for a transmembrane protein of the inner ear, has an important role in the evolution of bat echolocation (Dong et al. 2013; Zhang et al. 2013).

17.1.4.3 Understanding Bat Longevity

Bats have life spans approximately three times greater than other mammals in relation to their body size. The genus *Myotis* has many of the highest longevity records, with at least 13 species with a lifespan greater than 30 years. *Myotis brandtii* is the longest-lived species of bat with a reported lifespan of ~41 years, which is nine times longer than predicted for body size (4–8 g; Seim et al. 2013; Foley et al. 2018). A preliminary hypothesis of high longevity in bats was based on regulation of telomere maintenance to reduce cell senescence, which was mediated by telomerase, a reverse transcriptase that restores telomere repeat sequences. However, although qPCR and transcriptomic analyses do not show evidence of telomerase expression in *Myotis myotis,* individuals of this species do not appear to lose telomere length as they age, in contrast to *Rhinolophus ferrumequinum* and other mammals (Foley et al. 2018). These observations suggest that telomere maintenance is an autapomorphic adaptation of the *Myotis* lineage. Also, differential expression analysis of blood has revealed that telomerase is not the enzyme responsible for telomere regulation as suggested; instead, evidence indicates that genes involved with DNA repair pathways (*ALT, ATM, MRE11A, RAD50*, and *WRN*) may contribute to reducing cell senescence in bats (Foley et al. 2018). Genomic and transcriptomic analyses of *Myotis brandtii* have unveiled unique mutations in the insulin-like growth factor that might be involved in their extraordinary longevity. It has also been suggested that hibernation and low reproductive rate are factors that extend longevity in *Myotis* (Seim et al. 2013).

17.1.4.4 Adaptive Evolution of Bat Immunity

Among the adaptive traits in flying mammals, it has been suggested that bats have evolved a unique and extremely polymorphic immune system as a result of constant ancient interactions with pathogens, especially viruses (Papenfuss et al. 2012; Ng et al. 2016). It is assumed that genes involved with virus immune response, such as the major histocompatibility class I genes (MHC-I), interferons, and natural killer cells have an extreme number of functional and polymorphic variants among bats. To date, there are only two complete molecular studies on the immune repertory genes in a bat, both of which focused on *Pteropus alecto*. MHC-I genes have insertions of three and five amino acids in the α1 domain, which is encoded by exon 2 and is responsible for peptide recognition and binding. These insertions might provide an advantage in recognizing larger peptides or provide another adaptive advantage for antigen recognition (Papenfuss et al. 2012; Ng et al. 2016).

There is evidence of several gene family expansions in yinpterochiropteran bats and many of these are involved in immune response pathways. Discovery of a gene family of natural killer cell receptors and type I interferons in *Rousettus aegyptiacus* has led to the development of a novel strategy for inhibitory immune response against viruses. A new hypothesis to understand why bats are apparently resistant to many viruses suggests that this immunity relies on tolerance to viral infection instead of having extraordinary mechanisms of defense (Pavlovich et al. 2018). Finally, a comparative analysis of genomes and transcriptomes revealed that genes involved in immune system response are the ones with stronger evidence of positive selection because of the constant selective pressure exerted by pathogens (Seim et al. 2013; Hawkins et al. 2019).

17.1.5 Future of Bat Genomics

Forty-three years after Sarich’s talk, Sonja Vernes held a meeting during the 46th NASBR conference in San Antonio, Texas in 2016, where the BAT1K genomics project (https://bat1k.ucd.ie/) was presented. This ambitious project has the objective of generating high quality chromosome-level genomes of all bat species (Teeling et al. 2018). It is currently in the first phase to sequence one species from each of the 21 families. The second phase is to obtain genus-level coverage and the third phase is to sequence the genome of the >1,400 currently known species of bats.

To date there are ~32 bat species representing ten families with a genome or transcriptome dataset (Table 17.1). With sequencing costs decreasing constantly, the number of sequenced species will inevitably increase, and the understanding of adaptive traits and the evolution of these flying mammals will be more robust and

Table 17.1 Bat species with whole genome and/or whole transcriptome assemblies available in the National Center for Biotechnology Information (NCBI) repository (https://www.ncbi.nlm.nih.gov/; December 2019)

	Family	Species	Data type	Authors
Yinpterochiroptera	Hipposideridae	*Hipposideros armiger*	Genome	Dong et al. (2017)
		Hipposideros galeritus	Genome	*Unpublished*
	Megadermatidae	*Megaderma lyra*	Genome	Parker et al. (2013)
	Pteropodidae	*Eidolon helvum*	Genome	Parker et al. (2013)
		Eonycteris spelaea	Genome, transcriptome	Wen et al. (2018)
		Hypsignathus monstrosus	Transcriptome	Hawkins et al. (2019)
		Macroglossus sobrinus	Genome	*Unpublished*
		Pteropus alecto	Genome, transcriptome	Zhang et al. (2013) Papenfuss et al. (2012)
		Pteropus vampyrus	Genome	*Unpublished*
		Rousettus aegyptiacus	Genome, transcriptome	Lee et al. (2015) Pavlovich et al. (2018)
	Rhinolophidae	*Rhinolopus ferrumequinum*	Genome, transcriptome	Parker et al. (2013) Lei et al. (2014)
		Rhinolopus sinicus	Genome	Dong et al. (2017)
Yangochiroptera	Emballonuridae	*Peropteryx macrotis*	Transcriptome	Moreno et al. (2019)
	Miniopteridae	*Miniopterus natalensis*	Genome	Eckalbar et al. (2016)
		Miniopterus schreibersii	Genome, transcriptome	*Unpublished*, Wang et al. (2017)
	Molossidae	*Nyctinomops laticaudatus*	Transcriptome	Moreno et al. (2019)
		Tadarida brasiliensis	Genome, transcriptome	*Unpublished*
	Mormoopidae	*Mormoops blainvillei*	Genome	*Unpublished*
		Mormoops megalophylla	Transcriptome	Moreno et al. (2019)
		Pteronotus parnelli	Genome	Parker et al. (2013)
	Phyllostomidae	*Artibeus jamaicensis*	Transcriptome	Shaw et al. (2012) Moreno et al. (2019)
		Desmodus rotundus	Transcriptome	*Unpublished*

(continued)

Table 17.1 (continued)

	Family	Species	Data type	Authors
		Micronycteris hirsuta	Genome	*Unpublished*
		Phyllostomus discolor	Genome	*Unpublished*
	Vespertilionidae	*Eptesicus fuscus*	Genome	*Unpublished*
		Myotis brandtii	Genome, transcriptome	Seim et al. (2013)
		Myotis davidii	Genome	Zhang et al. (2013)
		Myotis keaysi	Transcriptome	Moreno et al. (2019)
		Myotis lucifugus	Genome	*Unpublished*
		Myotis ricketti	Transcriptome	Dong et al. (2013)
		Myotis rufoniger	Genome	Bhak et al. (2017)
		Pipistrellus pipistrellus	Genome	*Unpublished*

reliable. By integrating genomic and transcriptomic analyses, we can have a more accurate perspective of the genes that are regulating biological processes. The pioneering macromolecular biochemical methods from a half century ago opened the door to the molecular study of bats and formed evolutionary hypotheses that are being tested today from direct sequencing of DNA. The genome gives us the repertoire of genes that species have, whereas the transcriptome allows us to understand which of these genes are functional in these processes and how they are differentially expressed according to different ecological scenarios related to feeding habits, hibernation, and echolocation.

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Chapter 18
A Global Review of Phylogeographic Studies on Bats

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Abstract Phylogeography focuses on understanding the mechanisms that have led to the geographic distribution of genetic lineages within species, and studies of mammals have had an important role in its development. Bats are the second most diverse order of mammals; however, they are the subject of fewer phylogeographic studies than less diverse orders of mammals. Herein, we review the global state of phylogeographic bat research. Mitochondrial DNA loci are the most popular molecular markers, and the majority of studies describe geographic patterns of genetic variation. Many phylogeographic surveys were done in the Palearctic (mainly in the family Vespertilionidae), but more species have been studied in the Afrotropics and Neotropics (mainly in Pteropodidae and Phyllostomidae, respectively). Pleistocene climatic change is the main factor that has shaped the genetic diversity of species, but

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geographical and ecological factors are other important drivers of intraspecific differentiation. More intraspecific phylogeographic studies on bats are needed, but it is also necessary to develop comparative, integrative, and statistical approaches. Bats are excellent models for addressing evolutionary, ecological, and theoretical questions, given their world-wide distribution and their great biological heterogeneity. Annual meetings of the North American Society for Bat Research (NASBR) have contributed to the development of this field of molecular evolution, and we propose some future directions for phylogeographic research on bats.

Keywords Bibliometrics · Chiroptera · DNA · Evolution · Phylogeography

18.1 Introduction

Phylogeography focuses on studying the geographic distribution of genetic lineages, particularly at the intraspecific level, or between closely related species. Its main goal is to understand the causal factors and mechanisms that contribute to the divergence of populations and lead to speciation (Avise et al. 1987; Avise 2000; Eckert 2011). This discipline has grown substantially since its formal origin in 1987 (Avise 2009; Hickerson et al. 2010), which is reflected in the more than 3000 articles published during its first 20 years (Beheregaray 2008). Up until December 2017, 15,768 studies listed in the Web of Science database were retrieved with the search term “phylogeography” (Riddle and Jezkova 2019), and to date (August 2019) 2729 new works have been recorded in the same site, for a total of 18,497 records.

Initially, phylogeography was based on inferring historical events by comparing phylogenetic tree topologies and population genetic analyses with the geographical distribution of specimens (Avise et al. 1987; Avise 2000). Technological and theoretical advances have allowed for an increase in the scope of phylogeographic surveys, and after more than 30 years, the direction of phylogeographic research and even some major ideas about evolutionary processes have changed and diversified. For example, it is now possible to evaluate different scenarios of gene flow that promote speciation (Morales et al. 2017), to understand global patterns of evolution by analyzing enormous quantities of published information through automated big data phylogeographic studies (Carstens et al. 2018), or even to use predictive phylogeography to analyze environmental, taxonomic, and genetic data from co-distributed taxa with known phylogeographic histories to predict the cryptic/non-cryptic nature of unknown species (Espíndola et al. 2016).

Bats (order Chiroptera) represent the second most diverse mammalian order in the world. With over 1400 species, they are found on all continents with the exception of Antarctica (Burgin et al. 2018). Bats exhibit a wide range of morphologies, life histories, behaviors, and ecological characteristics, making them an ideal group to test multiple phylogeographic hypotheses (Nowak 1991; Altringham 2011; Taylor 2018). For example, studies on some species of bats show low levels of population structure across wide geographic distributions, while in others there are strong signals of genetic structuring even at small geographic scales (Ditchfield 2000; Russell et al. 2007; Clare 2011; Hernández-Dávila et al. 2012; Lim and Lee 2018; Patterson et al. 2019). These contrasting patterns in the distributions of genetic diversity, and the processes that generated them, are the consequence of the great biological and ecological heterogeneity within Chiroptera (Miller-Butterworth et al. 2003; Meyer et al. 2009; Olival 2012; Carstens et al. 2018).

In this chapter we present the general state of phylogeographic studies on bats from throughout the world, using a literature search of published articles during the past 32 years, the period in which this area of research has been recognized as an independent discipline. Also, after 50 years of annual meetings of the North American Society for Bat Research (NASBR), we discuss the relevance of this conference to the phylogeographic analysis of bats. In particular, we aimed to answer four main questions: (a) How much research exists and what does it encompass? (b) Which bat families and geographic areas are the most studied? (c) What are the main drivers of genetic differentiation in bats? and (d) How has NASBR participated in the dissemination of knowledge in phylogeographic bat research? Finally, this review concludes with an evaluation of challenges and future perspectives.

To achieve these goals, we searched in specialized databases (BioOne, Elsevier, Highwire, Iris, JSTOR, Pubmed, Scopus, SpringerLink, Wiley Online, Web of Science, and Zoological Records) for phylogeographic studies, using the terms "phylogeo*" plus "Chiroptera" or "bat" (searched in July 2019). We examined each result and retained only the publications in which the terms "phylogeography", "phylogeographic", or similar terms were found in the title, abstract, or keywords. Additionally, we included works that did not include the search terms in the title, abstract, or keywords, but whose goals, methodology or results were based on phylogeographic analyses. We followed Burgin et al. (2018) as the taxonomic reference and updated the reported species name in each work. In order to analyze the impact of NASBR meetings on phylogeographic studies, we used similar search methods for the programs of annual symposia from 1970 to 2018, and we also included all works presented in two thematic sessions on phylogeography in 2007 and 2013.

18.2 Current General State of Phylogeographic Studies on Bats

Papers we compiled show some general global patterns of bat phylogeographic research. We found 123 scientific papers published between 1991 and 2019 (Appendix S1), and more than half were published in the journals *Molecular Ecology*, *Acta Chiropterologica*, *Journal of Biogeography*, *Journal of Mammalogy*, *Molecular Phylogenetics and Evolution*, and *Biological Journal of the Linnean Society*. However, we found fewer phylogeographic bat papers than were reported for bats in the

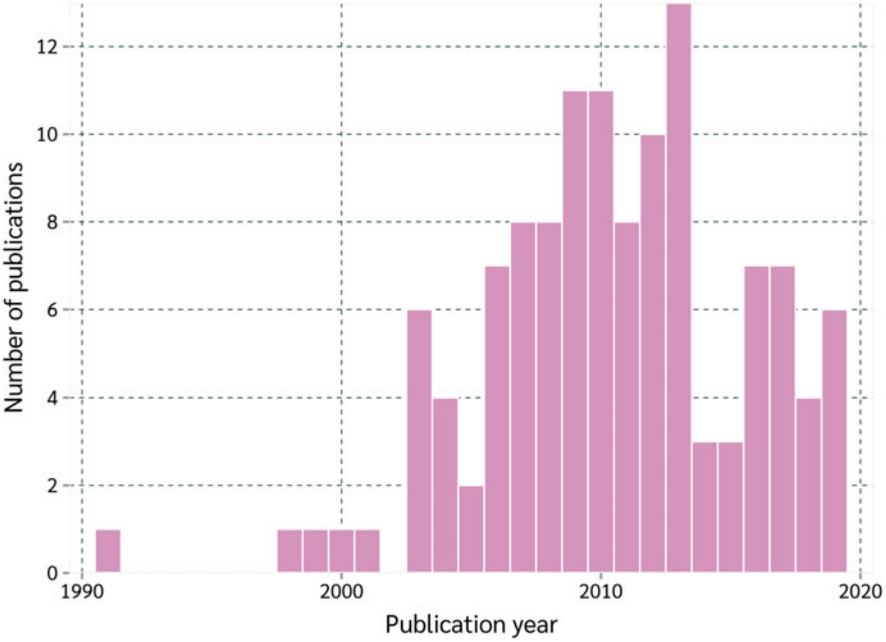

Fig. 18.1 Number of phylogeographic studies on bats per year

most recent review about phylogeographic studies in mammals (Riddle and Jezkova 2019). Different methodologies and a finer filtering of the data in our review likely explain this difference in results.

The first bat phylogeography paper recovered in our search was a study on two species of Neotropical fruit-eating bats in the genus *Artibeus* (Phillips et al. 1991). We found that the initial increase in phylogeographic bat publications per year occurred in 2003, but it decreased from a high of 13 after 2013 (Fig. 18.1). The number of sampled individuals per species per study (average = 75.34, range = 1–1003) is larger than the number of sampled localities (average = 15.91, range = 1–131) (Appendix S1). A similar relationship between number of sampled individuals and number of sampled localities was reported in mammalian phylogeographic studies, which is likely because researchers collect multiple individuals in localities that are selected to be optimized across the range of the taxon in an attempt to maximize the genetic diversity sampled within species (Riddle and Jezkova 2019).

Regarding molecular markers used in phylogeographic bat studies, mitochondrial DNA (mtDNA) sequences were the most common, used in 118 (95.93%) of the published works (average number of mitochondrial loci used per species = 1.30, range = 1–5). Since the emergence of phylogeographic surveys in 1987, mtDNA has been useful to characterize genetic diversity and estimate demographic parameters (Moritz 1994). Several factors have contributed to the widespread use of mtDNA as a molecular marker. Each individual cell typically has multiple identical copies of mitochondria, which greatly facilities polymerase chain reaction (PCR) protocols. However, each cell has only one nucleus with loci that are biallelic and may require more work and expense (cloning, computational phasing, etc.) to produce allelic sequences. Mitochondrial DNA has faster mutation rates that produce high nucleotide sequence variation (compared with many nuclear loci), and mtDNA is haploid and mainly uniparentally inherited, so it allows for faster lineage sorting than nuclear sequences (Avise 2009). Although mtDNA includes 37 linked genes plus a control region where replication is initiated (Avise 2009), the main mtDNA marker used for bats is cytochrome b (cytb). Genetic distances in cytb between sister species has been used as a reference point in making decisions concerning species-level distinctions (Bradley and Baker 2001).

Another commonly-used mtDNA locus is cytochrome oxidase I (COI), which is frequently employed for DNA barcoding (a tool for species identification and discovery using the comparison of inter- and intraspecific sequence divergence; Clare et al. 2011). However, some considerations must be taken into account because species identification based on mitochondrial loci require additional data, such as ecological, behavioral, morphological, or demographic information, to avoid under- or overestimating the number of studied species (Dávalos and Russell 2014). Other commonly-used mtDNA loci are sections of the control region that include the most rapidly evolving part of the mtDNA (Sbisa et al. 1997). All these reasons make mtDNA sequences one of the most abundant molecular markers in database sequence repositories such as Genbank.

After mtDNA, the second most used molecular markers were microsatellites, which were analyzed in 33 (26.82%) of the surveys, and then nuclear sequences, which were analyzed in 14 (11.38%) of the studies (average number of microsatellite loci used per species = 10.91, range = 5–23; average number of nuclear sequence loci used per species = 3.18, range = 1–12). Again, our results differ from those of Riddle and Jezkova (2019), who state that there were no phylogeographic bat surveys in which microsatellites were used. Microsatellites were first analyzed 8 years after the first recorded phylogeographic work in bats (Worthington Wilmer et al. 1999), and nuclear sequences were first used 6 years later (Piaggio and Perkins 2005). Microsatellite data have been commonly interpreted as better reflecting current processes, compared to mtDNA, which is influenced more by historical events (Ruedi and Castella 2003).

The use of nuclear sequences was hampered by technical and biological hurdles (the relatively slow mutation rate, presence of recombination, and the relative difficulty and increased cost of sequencing diploid genotypes; Avise 2009). But with the ongoing development of different methods (e.g., Stephens and Donnelly 2003), the use of nuclear sequences is more common now, with the most analyzed gene being RAG2 for bats. Even though the use of nuclear DNA (nDNA) has been gradual, many current surveys include both mtDNA and nDNA markers because their contrasting properties of different modes of inheritance and rates of evolution allow for a more robust and comprehensive understanding of species histories (Flanders et al. 2009). Lastly, other molecular markers such as restriction fragment length polymorphisms (RFLP), sequences from the Y chromosome, random amplification of polymorphic DNA (RAPD), amplified fragment length polymorphisms (AFLP), and ultraconserved elements (UCE) have been lesser used molecular markers in phylogeographic bat surveys, possibly because of their lower level of resolution, difficulty of cross-study comparisons, and issues with replicability, data analysis, or automation (Schlötterer 2004).

The majority of the papers we found described phylogeographic patterns of single taxa. After intraspecific descriptions, some of these surveys (and others that did not include intraspecific descriptions) contrasted patterns among taxa, and they were considered as comparative studies (18 papers that identified commonalities in biogeographic history based on multiple co-distributed species) (Beheregaray 2008). However, another 11 papers included more than one taxon but could not be considered comparative studies because they mainly included phylogenetically related species and/or taxa with nonoverlapping distributions. These results indicate that in the case of bats, many investigations are focused on phylogeographic structuring or the evolutionary history of single species, as was previously reported by Beheregaray (2008), who concluded that mammals are the taxonomic class with the highest percentage of taxon-specific studies.

Comparative phylogeography has been useful to recognize biogeographic (Arbogast and Kenagy 2001; Zink 2002), ecological (Olival 2012), and evolutionary patterns (Carstens et al. 2018), to understand emerging disease ecology (Olival 2012; Hassanin et al. 2016), and to identify genetically divergent areas for conservation (Moritz and Faith 1998). Additionally, more integrative studies are needed for bats because we identified <20 papers that included ecological and/or morphological analyses with genetic analyses (Table 18.1). There have been technological and theoretical advances in phylogeography that could promote its integration with other fields such as ecological niche modeling, ecological speciation, analysis of morphological and/or functional traits, natural selection, or even studies of community assembly. These integrative approaches could answer questions about how climate, geography, and ecological interactions drive the evolution of species and communities (Hickerson et al. 2010).

Phylogeographic bat studies that have included ecological data have analyzed patterns of geographic variation (Ratrimomanarivo et al. 2009), determined whether current climatic differentiation among haplogroups influences the distribution of genetic variation (Lamb et al. 2008; Hernández-Canchola and León-Paniagua 2017; Najafi et al. 2018), and addressed the effect of past and future climatic change on distribution and genetic diversity (Razgour et al. 2013). For the most part, ecological phylogeographic surveys have analyzed the effect of paleo-climatic distributions on current genetic structure (Bilgin et al. 2016; Carstens et al. 2018). Phylogeographic studies that have included morphological data have been useful to analyze patterns of geographic variation (Ratrimomanarivo et al. 2009), but mainly they have been used to propose taxonomic changes or to describe new species (Goodman et al. 2010; Ith et al. 2016). Even though many auxiliary fields could be incorporated into phylogeographic studies, it is important to at least consider ecological and morphological variation, since it has been suggested that for bats, environmental variation may contribute to evolutionary processes and the distribution of genetic and

Table 18.1 Description of 123 phylogeographic bat studies analyzed in this review

Family	n studies	Molecular analyses	Ecological analyses	Morphological analyses	mtDNA sequences	Microsatellites	nDNA sequences	RFLPs	Y chromosome sequences	RAPDs	AFLPs	UCEs
Cistugidae	0	–	–	–	–	–	–	–	–	–	–	–
Craseonycteridae	0	–	–	–	–	–	–	–	–	–	–	–
Emballonuridae	4	4	0	0	4	0	0	0	1	0	0	0
Furipteridae	0	–	–	–	–	–	–	–	–	–	–	–
Hipposideridae	3	3	0	0	3	1	0	0	0	0	0	0
Megadermatidae	1	1	0	0	1	1	0	1	0	0	0	0
Miniopteridae	11	11	1	1	11	2	1	0	0	0	0	0
Molossidae	14	14	3	4	14	1	2	0	0	1	0	0
Mormoopidae	4	4	0	0	4	0	0	0	0	0	0	0
Mystacinidae	2	2	0	0	2	0	0	0	0	0	0	0
Myzopodidae	1	1	0	0	1	0	0	0	0	0	0	0
Natalidae	2	2	0	0	2	0	0	0	0	0	0	0
Noctilionidae	3	3	0	0	3	0	1	0	0	0	0	0
Nycteridae	0	–	–	–	–	–	–	–	–	–	–	–
Phyllostomidae	24	24	1	1	22	0	2	4	1	0	0	0
Pteropodidae	16	16	1	1	16	7	2	0	0	0	0	0
Rhinolophidae	14	14	4	1	13	6	3	0	0	0	0	0
Rhinonycteridae	2	2	0	0	2	0	0	0	0	0	0	0
Rhinopomatidae	1	1	0	0	1	0	0	0	0	0	0	0
Thyropteridae	0	–	–	–	–	–	–	–	–	–	–	–
Vespertilionidae	44	44	3	3	42	15	6	0	0	0	1	1
Totals	146	146	13	11	141	33	17	5	2	1	1	1

The total number of studies, as well as the number of molecular, ecological and morphological studies per family are shown. Also includes the number of studies that used various molecular markers. Note that some papers analyzed more than one family, molecular marker, or used different analyses.

morphometric variation (Morales et al. 2016). Additionally, other fields such as acoustics could be useful to understand the evolutionary history of bats (Ith et al. 2016).

18.3 Taxonomic and Geographic Patterns

We found that most phylogeographic studies were in Vespertilionidae (44; Table 18.1), which is the most diverse and widely distributed family within Chiroptera (Burgin et al. 2018; Taylor 2018). Phyllostomidae (24), Pteropodidae (16), Molossidae (14), and Rhinolophidae (14) are other well-studied families, which also contain undescribed and cryptic taxa (Juste et al. 2004; Campbell et al. 2006; Larsen et al. 2013; Kuo et al. 2014; Hassanin et al. 2016; Lim and Lee 2018). Studies of these families have increased the number of species within Chiroptera based on both *de novo* descriptions and splitting of previously recognized taxa (Burgin et al. 2018). However, less than 50% of the species in these families have been studied (Fig. 18.2), so there is potential for more unrecognized species to be discovered. We did not find any phylogeographic surveys in species-poor families such as Craseonycteridae, Cistugidae, Furipteridae, Thyropteridae, and Nycteridae. Phylogeographic studies in these families are needed because they include species having restricted distributions and representing unique evolutionary histories.

To explore the spatial patterns of phylogeographic research in bats, we assigned each study to a broad biogeographic region according to its stated study area. We followed the global zoogeographic realms proposed by Holt et al. (2013), and compared the number of studies per region with the total number of species studied per region (Fig. 18.3). More species have been studied in the Afrotropics (90) and Neotropics (88), a result driven largely by two broad-scale multispecies studies in the tropics (Hassanin et al. 2016; Lim and Lee 2018). However, more studies focus on taxa in the Palearctic region (42). Palearctic surveys were mainly located in Europe, often focused on vespertilionid bats, and in many cases involved researchers from these countries analyzing species in their own and neighboring countries. Several Palearctic studies examined taxonomic uncertainties or made conservation recommendations, but the overarching focus was testing evolutionary processes such as the effect of Pleistocene climatic oscillations and past refugia (Rossiter et al. 2007; Çoraman et al. 2013; Bogdanowicz et al. 2015). In the Afrotropical and Neotropical regions, the general research focus was different than in the Palearctic. The most studied family in each region was Pteropodidae and Phyllostomidae, respectively, and many studies were not by local researchers; instead they were mainly researchers based in North America or Europe. Some species were analyzed with the goal of reconstructing evolutionary processes (Martins et al. 2009; Holanda et al. 2012; Naidoo et al. 2016; Riesle-Sbarbaro et al. 2018), but the majority of Afrotropical and Neotropical phylogeographic studies were focused on the detection of unrecognized intraspecific lineages

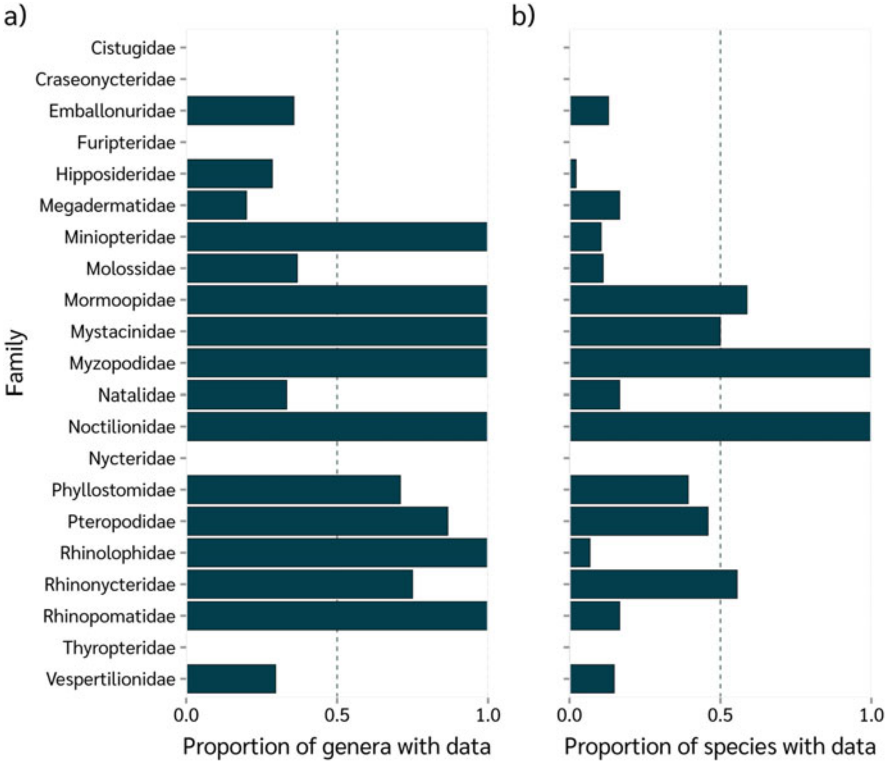

Fig. 18.2 Proportion of genera (**a**) and species (**b**) that have been studied in phylogeographic analyses of bats

(Ditchfield 2000; Clare 2011; Hassanin et al. 2016; Lim and Lee 2018; Patterson et al. 2019).

We also recorded the country in which the primary institution for each of the authors is located, and found that the countries with the most authors were the United States and the United Kingdom, with 38 and 21 respectively. However, of the 143 different countries sampled for phylogeographic studies, the most studied were Mexico, Greece, Turkey, and Spain with 25, 22, 21, and 18 studies, respectively (Fig. 18.4). The geographical distribution of sampled countries and analyzed regions is similar to patterns of higher mammalian and chiropteran species richness in the tropics (Burgin et al. 2018; Riddle and Jezkova 2019). But there is a misalignment between research effort, authors' institutions, and the distribution of bat diversity, which is often determined by geopolitical, historical, and linguistic relationships between countries, and with scientific investment related to wealth (Verde Arregoitia and González-Suárez 2019).

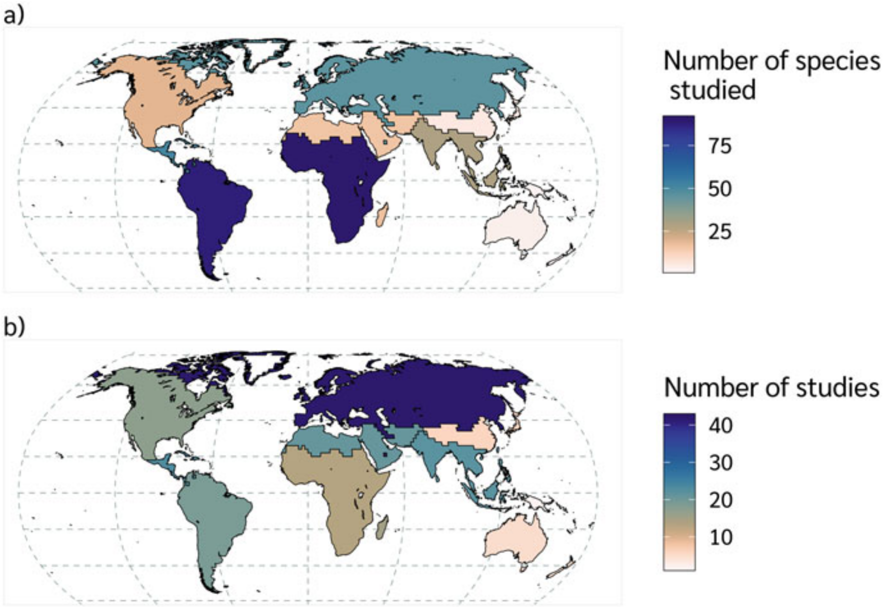

Fig. 18.3 Global distribution of phylogeographic studies on bats. (**a**) Number of species analyzed per region. (**b**) Number of studies performed per region. Global zoogeographic realms based on Holt et al. (2013)

18.4 How and When Were Closely Related Bat Lineages Shaped by Evolution?

The Quaternary stands out as the main period that has promoted detectable intraspecific genetic structuring. All studied species in the families Hipposideridae, Megadermatidae, Miniopteridae, Molossidae, Mormoopidae, Mystacinidae, Myzopodidae, Noctilionidae, and Rhinolophidae, as well as most species in Phyllostomidae, Pteropodidae, and Vespertilionidae were affected during the Quaternary (Table 18.2). This period began *c.* 2.58 Ma and includes the most recent and greatest cyclical climatic changes (Gibbard et al. 2010). Its phylogeographic relevance had already been recognized in bats (Carstens et al. 2018), as well as in other small mammals such as rodents (Riddle and Jezkova 2019) and many other taxa (Hewitt 2000; Riddle 2016). Given their global distribution, bats have been useful to analyze the effect of Quaternary climatic changes on their distribution, demographic history, and genetic diversity. Species that inhabit higher latitudes show strong signals of bottlenecks, and isolation into lower-latitude refugia followed by population expansion (Moreno-Letelier and Piñero 2009; You et al. 2010; Boston et al. 2015). In tropical regions, the biological consequences are less dramatic but more heterogeneous and complex due to climatic patterns compounded by topography,

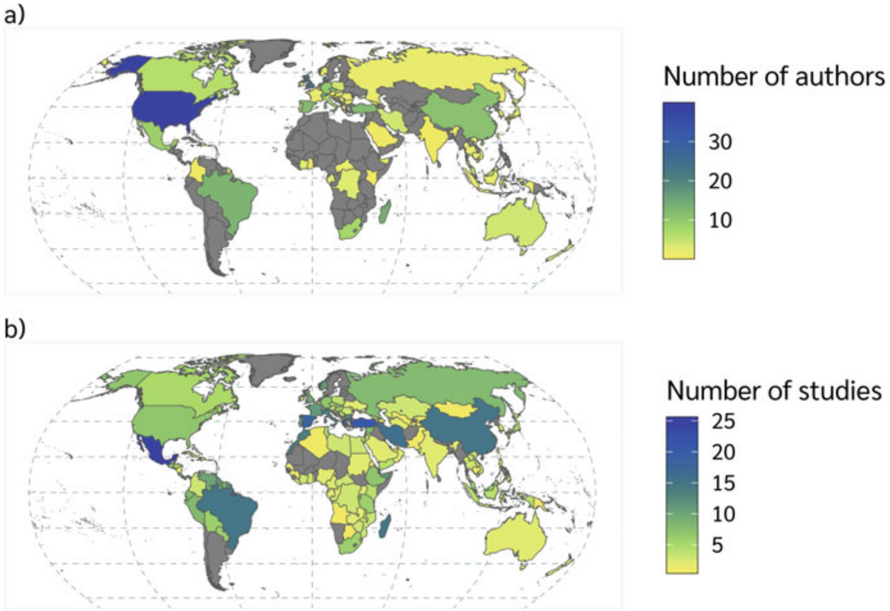

Fig. 18.4 Global distribution of authors and sampling of phylogeographic studies on bats. (**a**) Study output per country, based on primary institution reported. (**b**) Number of studies that used bat samples per each country

which affects the biota both latitudinally and altitudinally (Ramírez-Barahona and Eguiarte 2013; Lamb et al. 2008; Guevara-Chumacero et al. 2010).

Geographic factors have also driven genetic structuring in bats. Oceans (Pulvers and Colgan 2007; Russell et al. 2016) and mountains (Kuo et al. 2014; Dias et al. 2017) are the main barriers to gene flow, whereas deserts and rivers have also had an effect on the distribution of genetic diversity in some bats (Armstrong 2006; Goodman et al. 2010). Bats are an interesting model group to test hypotheses about the effect of geographic features on the evolution of flying biota, and the comparison among phylogeographic works in multiple co-distributed species could generate a connection between phylogeography and historical biogeography (Kidd and Ritchie 2006). Understanding isolation and divergence in a geographical context is highly relevant because geographical models of speciation depend on the area and the level of gene flow (Kisel and Barraclough 2010).

Ecological processes also promote the distribution of genetic variation (Gutiérrez-Rodríguez et al. 2011) and are an important factor in many speciation events (Avise 2000) because differentiation of the environmental niche often occurs at the same time as speciation (Warren et al. 2008). Analyses of these processes have been developed more recently, and some bat phylogeographic surveys have included them (Morales et al. 2016; Hernández-Canchola and León-Paniagua 2017). More investigations are critical to understand the role of ecological factors in the speciation process, and to detect cryptic lineages in morphologically conserved taxa and

Table 18.2 Main divergence time of phylogeographic patterns detected per bat family. Summary of the proportion of species affected during the Quaternary or Neogene and the average number of intraspecific and cryptic lineages per species

Family	Porportion of species affected during Quaternary	Porportion of species affected during Neogene	Average number of detected intraspecific lineages	Average number of detected cryptic taxa
Emballonuridae	–	–	3	1
Hipposideridae	1	0	4	0
Megadermatidae	1	0	4	0
Miniopteridae	1	0	1.78	0.38
Molossidae	1	0	2.58	0.33
Mormoopidae	1	0	2	0.17
Mystacinidae	1	0	6	6
Myzopodidae	1	0	2	1
Natalidae	–	–	1	0
Noctilionidae	1	0	1.67	1
Phyllostomidae	0.96	0.04	2.22	0.28
Pteropodidae	0.87	0.13	1.34	0.13
Rhinolophidae	1	0	3.64	0
Rhinonycteridae	–	–	1.2	0.4
Rhinopomatidae	–	–	4	0
Vespertilionidae	0.99	0.01	2.78	0.35

identify limits among species in early stages of speciation (Wiens 2004; Broennimann et al. 2012; Hu et al. 2016).

Range expansion (Evin et al. 2011; Pavan et al. 2013), geological or landscape transformation (Lloyd 2003; Lack et al. 2010), and human activities (Ortega et al. 2009) are other sources of genetic differentiation that affect the distribution of genetic diversity within Chiroptera. Even though many small or low vagility terrestrial mammal species show deep phylogeographic structure (Avise 2000), it is important to note that among bat species there are many different levels of phylogeographic structure. For example, almost half of the bat papers used in our study do not show signals of phylogeographic differentiation, but in the other cases, 2–10 intraspecific lineages were detected (Table 18.2). Within Chiroptera, the levels of phylogeographic structuring and evolutionary history are the consequence of historical events and complex geography. Patterns of phylogeography are also influenced by ecological, behavioral, and life-history traits such as environmental requirements, interactions with other species and resources, vagility, population size, roosting, mating behaviors, site fidelity, allegiance to social groups, migration, and wing morphology (Avise 2000; Ditchfield 2000; Olival 2012; Carstens et al. 2018).

18.5 NASBR Impact

Since 1970, we identified 60 contributions presented at 20 NASBR meetings between 1994 and 2018 that focused on phylogeography (Appendix). Talks on "The phylogeography of bats of the Atlantic forest of Brazil" (Ditchfield) and "Phylogeography of *Leptonycteris curasoae* using mtDNA sequences" (Wilkinson and Fleming) were the first phylogeographic discussions at NASBR meetings. On average, there were three phylogeographic studies per meeting from 1994 to 2018. But two meetings in 2007 and 2013 were jointly held with the International Bat Research Conference and had special thematic sessions on phylogeography, which accounted for almost half of the contributions (43%). We did not see any meaningful change in the number of phylogeographic studies presented over time, but hope that this number increases at future meetings. Without full abstracts for all meetings, we used text searching techniques to identify popular taxa in the phylogeography presentations. The most common family was Vespertilionidae: *Myotis* appeared in 16 titles and *Eptesicus* in four. The family Phyllostomidae appears in four titles, and all other taxa appear in three or fewer titles.

We identified two ways in which NASBR meetings have contributed to the development of phylogeographic studies in bats. Several works were presented during conferences and ultimately published (e.g., Ditchfield 2000; Campbell et al. 2004; Flanders et al. 2009). Presenting results and ideas at conferences offer an excellent opportunity to receive feedback in order to increase the potential impact of the work presented (Verde Arregoitia and González-Suárez 2019). We also found some works that used NASBR conferences as a forum to announce recent or upcoming research (e.g., Hulva et al. 2012; Lim and Lee 2018) to transmit new knowledge directly to other chiropteran experts without the additional delays often brought on by the publishing process of scientific journals. Phylogeographic surveys are relevant to NASBR because studies related to how many bat species there are, how they originated, and how genetic diversity is distributed concerns all bat researchers who are interested in systematics, ecology, conservation, and management.

18.6 Future Directions

Mammals have been an important taxon in the development of phylogeography (Avise 2000; Beheregaray 2008; Riddle and Jezkova 2019), but bats have not been studied as much as other mammalian orders. Only 12% of mammalian phylogeographic studies have focused on Chiroptera, whereas other less diverse orders have been analyzed more often (Cetartiodactyla with 21% and Carnivora with 18%; Riddle and Jezkova 2019). Considering that Chiroptera is the second most diverse mammal order, and that new taxa continue to be discovered and described (Burgin et al. 2018), more phylogeographic studies in bats are needed.

We found that the majority of published works are intraspecific and descriptive analyses, which are necessary in the most diverse regions where new mammalian species have been recognized (Burgin et al. 2018). However, more sampling is required in uncommon and species-poor taxa. It is also important to note that the most diverse regions are where the less studied bat families live. In addition, these families are found in the Southern Hemisphere and some developing countries in the Northern Hemisphere where phylogeographic studies are scarce for many taxa (Beheregaray 2008). We therefore highlight the relevance of international collaboration to understand how many bat species there are, as well as to include analyses that can answer questions related to their evolutionary histories.

Comparative, integrative, and statistical phylogeographic surveys must also increase. Fortunately, these kinds of works are starting to emerge in bats. For example, Carstens et al. (2018) used GenBank mitochondrial sequences to understand the global demographic response of bats to climatic change in the Pleistocene. They compared multiple species in an integrative approach, but also used statistical methods to compare different hypotheses. Bats could also be a model group to develop and validate new theoretical frameworks. For example, *Myotis* have been used to demonstrate that speciation occurs even in the presence of gene flow (Morales et al. 2017). The biological and ecological heterogeneity and world-wide distribution of bats make them amenable to test ecological, evolutionary, and theoretical questions.

Bats perform several invaluable ecosystem services, but approximately 15% of bat species are considered globally threatened with extinction by the IUCN, and 18% are Data Deficient (Voigt and Kingston 2016). In addition, many bat species are cryptic and cannot be easily identified based on obvious external features, and underestimating biodiversity can lead to poor management and conservation programs with unforeseen ecological consequences (Tsang et al. 2016). However, if phylogeographic studies included other data such as ecological, morphological, echolocation, or behavioral information, this would help identify unrecognized taxa, while also avoiding taxonomic inflation, which also has consequences in bat conservation. To guarantee the long-term viability of ecosystems, it is important to conserve the genetic variation within and among populations, and to maintain independent evolutionary processes because many populations include local adaptations (Vázquez-Domínguez and Vega 2006). This is relevant in bats because almost all bat families have intra-specific differentiated lineages (Table 18.2). Additionally, we must improve the impact of phylogeographic research on conservation plans because they have been underutilized in conservation genetics (Médail and Baumel 2018).

After 50 years of NASBR conferences, it is clear that members of this organization have participated in the growth and development of phylogeographic research on bats. Since the emergence of the first studies, many discoveries related to systematics, evolution, ecology, biogeography, and conservation genetics have been found using phylogeographic analyses. As theoretical and technological developments advance this field, and new collaborations arise during upcoming annual meetings, the future of phylogeographic research on bats is promising.

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Phylogeographic Bat Contributions Presented at NASBR Meetings Examined in This Review

	Year	First author	Family	Taxa
1	1994	Ditchfield	–	–
2		Wilkinson	Phyllostomidae	*Leptonycteris curasoae*
3	1995	Ditchfield	–	–
4	1998	Williams	Vespertilionidae	*Eptesicus fuscus*
5	1999	Byrnes	–	–
6		Russell	Molossidae	*Tadarida brasiliensis*
7	2000	Turmelle	Vespertilionidae	*Eptesicus fuscus*
8	2001	Cambell	Pteropodidae	*Cynopterus brachyotis*
9		Dewey	Vespertilionidae	*Myotis*
10	2002	Rodriguez	Vespertilionidae	*Myotis californicus*, *Myotis ciliolabrum*
11	2003	Hoffmann	Phyllostomidae	*Carollia*
12		Russell	Molossidae	*Tadarida brasiliensis*
13		Turmelle	Vespertilionidae	*Eptesicus fuscus*
14		Weyandt	Vespertilionidae	*Antrozous pallidus*
15	2004	Fleming	Phyllostomidae	–
16		Russell	Molossidae	*Tadarida brasiliensis*
17		Vonhof	Vespertilionidae	*Myotis volans*
18	2005	Mantilla-Meluk	Phyllostomidae	*Urdoderma bilobatum*
19	2007	Boston	Vespertilionidae	*Nyctalus leisleri*
20		Dávalos	Phyllostomidae	–
21		Dool	Rhinolophidae	*Rhinolophus hipposideros*
22		Flanders	Rhinolophidae	*Rhinolophus ferrumequinum*
23		Flores-Martínez	Vespertilionidae	*Myotis vivesi*
24		Guevara-Chumacero	Mormoopidae	*Pteronotus davyi*
25		Hulva	Vespertilionidae	*Pipistrellus pipistrellus*
26		Miller Butterworth	Miniopteridae	*Miniopterus*
27		Parlos	Vespertilionidae	*Myotis velifer*
28		Puechmaille	Craseonycteridae	*Craseonycteris thonglongyai*
29		Ruedi	Vespertilionidae	*Myotis myotis*, *Myotis blythii*
30		Russell	Rhinonycteridae	*Triaenops*
31		Teeling	–	–
32		Van Den Bussche	Vespertilionidae	*Antrozous pallidus*
33		Vonhof	Thyropteridae	*Thyroptera tricolor*
34	2008	Vonhof	Thyropteridae	*Thyroptera tricolor*
35	2010	Wilkinson	Vespertilionidae	*Antrozous pallidus*
36	2011	Khan	Hipposideridae	*Hipposideros bicolor*
37		Magrini	Molossidae	*Tadarida brasiliensis*
38		Wilder	Vespertilionidae	*Eptesicus fuscus*
39	2012	Poythress	Vespertilionidae	*Myotis lucifugus*
40		Russell	Vespertilionidae	*Myotis lucifugus*

(continued)

	Year	First author	Family	Taxa
41		Wilder	Vespertilionidae	*Myotis lucifugus*
42	2013	Amorim	Molossidae	*Tadarida teniotis*
43		Bilgin	–	–
44		Herdina	Vespertilionidae	*Pipistrellus*
45		Hernández-Canchola	Phyllostomidae	*Sturnira lilium*
46		Hulva	Pteropodidae	*Rousettus aegyptiacus*
47		Larsen	–	–
48		Rossiter	Rhinolophidae	*Rhinolophus*
49		Russell	–	–
50		Siles	Phyllostomidae	*Micronycteris*
51		Soto-Centeno	–	–
52		Wilder	Vespertilionidae	*Myotis lucifugus*
53	2014	Wilder	Vespertilionidae	*Myotis lucifugus*
54	2015	Lim	–	–
55	2017	Ureel	Vespertilionidae	*Myotis austroriparius*
56	2018	Cortés-Delgado	Phyllostomidae	*Artibeus fraterculus*
57		Decker	Vespertilionidae	*Dasypterus intermedius*
58		Guevara-Chumacero	Mormoopidae	*Pteronotus psilotis*
59		Lim	–	–
60		O’Toole	–	–

Data not available (–)

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Part IX
Parasitology

Jorge Ortega

Research about parasitology in bats has been a recurring topic, especially in recent times due to the particular situation vis-à-vis COVID-19 we are going through. It is also a delicate subject that must be dealt with responsibly to provide the proper focus on the relationship that bats have with pathogens, so as not to overstate the sensationalized headlines often seen in media, but to provide a reasoned approach to the issue. This section of the book focuses primarily on giving a better understanding of bats as an appropriate taxonomic group to explore the effects of host biology on their co-evolution with pathogens. The three compendia span a wide range of parasitology including viral forms, bacteria and protozoa, and parasitic fungi.

The first chapter by Cheetham and Markotter summarizes the current knowledge on zoonotic viruses of potential origin in bats. In light of the COVID-19 pandemic, the paper points out the need to understand with scientific rigor the immunological characteristics of bats that allow them to sustain a quantity of viruses in their systems without showing apparent acute symptoms.

In the second chapter, Colunga-Salas and collaborators enlighten the reader about the interrelationships between bats and specific pathogens such as bacteria and protozoa. Despite the exhaustive review, there are few conclusive results that show bats as reservoirs of these pathogens. Likewise, the authors present a compilation of the studies presented in all of the NASBR meetings.

The last installment in this section describes levels of hyperparasitism presented among the final host (bats), which are parasitized by bat flies, which in turn have parasitically associated biotropic fungi. These multitrophic associations are addressed by Haelewaters and collaborators, where they point out the complexity of the interrelationships of various taxonomic levels and the parasitic trophic chains that can be linked in a relevant way among these species.

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Chapter 19
Bats as Reservoirs of Viral Zoonoses

Sonia Cheetham and Wanda Markotter

Abstract In the last few decades, a special interest in viruses hosted by bats arose after links with zoonoses of public health importance emerged. A dramatic increase in documented viral diversity in bats has occurred with an increasing difficulty in interpretation of results and risk assessments. In addition, the risk of spillover directly from bats or through other intermediate hosts is on the rise as human exposure results from habitat encroachment, human population expansion, deforestation and changes in climate and human behavior, such as increased bushmeat consumption, live animal markets, and cave exploration. The link between rabies and bats has been known for decades; however, there are many other viruses that also pose a threat with no prophylactic treatment or prevention measures existing yet. In addition, viruses have different routes of transmission and shedding may be seasonal. Our aim is to summarize what is known about important virus families implicated in zoonotic events with a bat origin. We include a discussion on potential immunological characteristics that allow bats to harbor many of these viruses without showing signs of disease and raise awareness on how to avoid exposure by considering different routes of exposure to infectious agents.

Keywords Bat immunology · Bat virome · *Coronaviridae* · *Filoviridae* · *Orthomyxoviridae* · *Paramyxoviridae* · *Rhabdoviridae* · Spillover · Viral reservoir · Viruses · Zoonotic viruses

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19.1 Introduction

In the last quarter-century, a dramatic expansion of research on viruses of bats occurred in response to human outbreaks of Hendra virus (1994), Nipah virus (1998), SARS coronavirus (CoV) (2002), MERS-CoV (2012) and more recently Ebola virus (2013, 2019); all with high morbidity and/or mortality rates and implicating a connection to bats. The reservoir host of the recent SARS-CoV-2 virus that causes COVID-19 pneumonia has not been confirmed, but the virus genome is most similar to a SARS-CoV-like coronavirus that is found in bats (Zhou et al. 2020). In 2008, there were about 2000 sequences deposited on Genbank of viruses identified in bats and over 100 publications of viruses related to bats (Olival et al. 2017). Ten years later, the number had increased to around 12,000 sequences and more than 400 publications for that year. A comprehensive resource on viruses in bats is available at http://www.mgc.ac.cn/DBatVir/ (Chen et al. 2014).

At least 27 viral families associated with bats have been identified (Table 19.1). The two families best represented on Genbank are *Coronaviridae* (36%) and *Rhabdoviridae* (24%), which account for most of the approximately 10,000 sequences. Taxonomically, almost half (45%) of the viruses are found in the bat family Vespertilionidae (Fig. 19.1). Geographically, most (37%) have been reported in Asia (Fig. 19.2). However, this information is based only on partial nucleic acid sequence detection, with very limited information on additional genome characterization, virus isolation, viral epidemiology and pathogenesis for most. The increase in surveillance using pan-virus family detection techniques, application of metagenomics and next generation sequencing has accelerated virus discovery in bats and the data has grown exponentially. Findings based solely on sequence information do not provide insight into the nature of the viral-host interactions and fail to address whether bats play an essential role in the epidemiology of these viruses.

So, are bats zoonotic-viral reservoirs? There is no easy answer to this question and the characteristics for a true viral reservoir are regularly debated. For the purpose of this review, we will define a reservoir as the host that maintains a viral agent within its population and is responsible for transmitting the agent to humans or indirectly through other animal species. Although there is no doubt that bats play an important role in the epidemiology of certain diseases (for example rabies), in other instances their involvement is less clear. Detection of the pathogen in the bats is just the first step, and to answer questions on reservoir status requires longitudinal studies that include virus isolation, understanding the route of transmission, tropism, and establishing links to human and animal outbreaks with appropriate virological evidence and viral pathogenesis. Viral isolation proved to be difficult for most bat viruses, limiting subsequent experimental infections. Other challenges that limit these kinds of experiments are ethics, costs, appropriate biosafety facilities and the existence of only a few closed bat-breeding colonies, which are essential for experimental infection studies. Thus, for most viruses, pathogenesis studies are missing, although they can provide invaluable data regarding tissue/cell tropism,

Table 19.1 Number of Genbank sequences from viral families found in bats

Viral family	#	%
Adenoviridae	356	3.44
Anelloviridae	1	0.01
Astroviridae	691	6.67
Bornaviridae	2	0.02
Caliciviridae	40	0.39
Circoviridae	243	2.35
Coronaviridae	3675	35.47
Filoviridae	111	1.07
Flaviviridae	211	2.04
Hantaviridae	56	0.54
Hepadnaviridae	77	0.74
Hepeviridae	14	0.14
Herpesviridae	232	2.24
Nairoviridae	22	0.21
Orthomyxoviridae	8	0.08
Papillomaviridae	58	0.56
Paramyxoviridae	986	9.52
Parvoviridae	161	1.55
Peribunyaviridae	31	0.3
Phenuiviridae	8	0.08
Picobirnaviridae	2	0.02
Picornaviridae	174	1.68
Polyomaviridae	67	0.65
Poxviridae	5	0.05
Reoviridae	278	2.68
Retroviridae	18	0.17
Rhabdoviridae	2832	27.33
Togaviridae	3	0.03

Source: http://www.mgc.ac.cn/cgi-bin/DBatVir/main.cgi; reproduced with permission

pathology or lack of, duration of viremia (if any), and route and duration of shedding. Serological studies have certain limitations because antibody responses may be difficult to interpret in bats and serological surveys only confirm exposure. In addition, cross-reaction between closely related viruses occurs and studies use different cut-off values and tests to report them, sometimes delivering contradictory results.

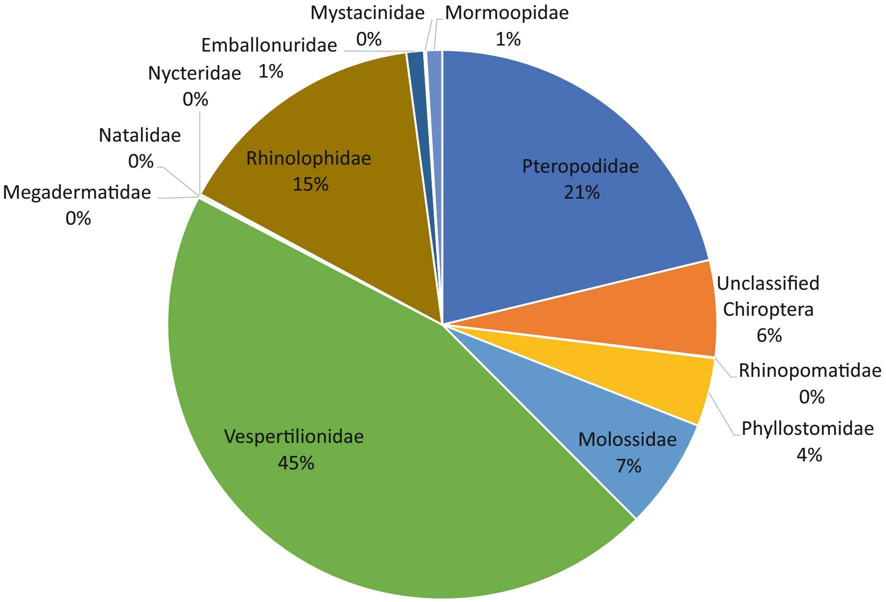

Fig. 19.1 Proportion of viral sequences found in each bat family. Source: http://www.mgc.ac.cn/cgi-bin/DBatVir/main.cgi; reproduced with permission

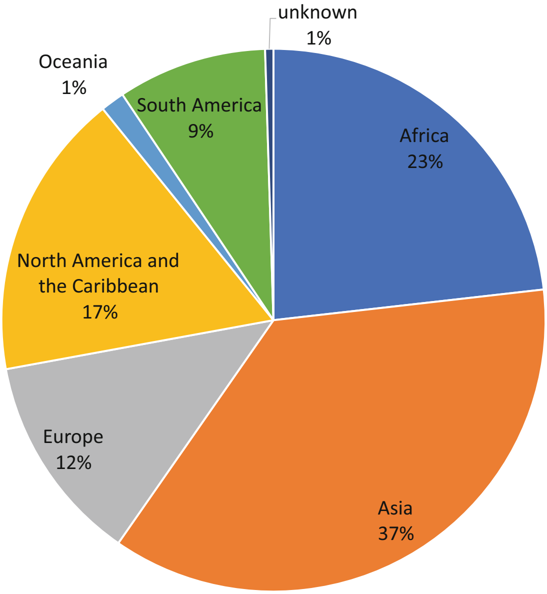

Fig. 19.2 Reports of viruses in bats by region. http://www.mgc.ac.cn/cgi-bin/DBatVir/main.cgi; reproduced with permission

19.2 Important Virus Families

During the rise of virus discovery in the 1940s, the possibility of bats being susceptible to zoonotic infections such as rabies, yellow fever, West Nile, and Newcastle, was described in the literature with Dr. R.L. Reagan at the University of Maryland being one of the pioneers. However, for the following decades, evidence of the importance of bats as possible reservoirs for zoonotic viruses other than rabies remained limited. Bats have now gained worldwide attention as hosts of diverse viruses, some with zoonotic potential including the *Paramyxoviridae, Coronaviridae, Filoviridae, Flaviviridae, Togaviridae* and *Orthomyxoviridae* families as well as many viruses in the *Bunyavirales*. The following sections are a brief summary of the most relevant viral families found in bats with established or potential zoonotic behavior. Other families/viruses found in bats are listed in http://www.mgc.ac.cn/DBatVir/, but our understanding of most of the viruses they carry is very limited and relies heavily on nucleic acid or serological data.

19.2.1 Rabies and Rabies Related Lyssaviruses

Rabies is one of the most studied viral infections in bats with the disease described thousands of years ago in Greek and Roman literature. However, the first report of a rabies infected cattle was only 120 years ago and this was subsequently linked to bat bites (Carini 1911). Since then, multiple isolations of rabies lyssavirus (RABV) have been made from the common vampire bat (*Desmodus rotundus*) in Central and South America with reported spillover into other species including fatal human infections. Insectivorous bat RABV was only described a few decades later in the 1950s in North America and research on transmission routes have continued sporadically since (Fenton et al. 2019; Venters et al. 1954).

Since then active surveillance studies reported a diverse number of bat species naturally infected with RABV and a wide geographic distribution of infected bats in North and South America (Gilbert 2018). The potential for aerosol transmission was documented by isolation of the virus from air samples and experimental studies indicated transmission to captive carnivores in caves harboring large colonies of Brazilian free-tailed bats (*Tadarida brasiliensis*) under very specific environmental conditions (Davis et al. 2007). However, contact with infected saliva, usually through a bite, is still the common route of transmission. Spillover from bats to wild and domestic carnivores occurs infrequently, however, there are some examples of spillover being maintained in striped skunk (Leslie et al. 2006) and grey fox populations in Arizona (Kuzmin et al. 2012). Since the elimination of canine rabies from the US (formally declared in 2007), the majority of human rabies cases have been linked to insectivorous bat RABV and mainly associated with the silver haired bat (*Lasionycteris noctivagans*) or Brazilian free-tailed bat species (Ma et al. 2018).

Other lyssaviruses are associated with unique geographical areas outside of the America's and specific bat species and are not a significant public health threat, although surveillance is limited (Markotter and Coertse 2018). Lyssaviruses cluster into three distinct phylogroups, with serologic cross neutralization occurring within each phylogroup, but not between them. Phylogroup I includes *rabies lyssavirus, European Bat Lyssavirus 1 and 2, Duvenhage lyssavirus, Australian bat lyssavirus, Aravan lyssavirus, Bokeloh bat lyssavirus, Gannoruwa bat lyssavirus, Irkut lyssavirus, Khujand lyssavirus, Taiwan bat lyssavirus and Kotalathi bat lyssavirus;* phylogroup II includes *Lagos bat lyssavirus, Mokola lyssavirus* and *Shimoni bat lyssavirus*; and phylogroup III includes *Lleida bat lyssavirus, Ikoma lyssavirus* and *West Caucasian bat lyssavirus.*

Although dogs are the main reservoir of rabies globally, and responsible for most human infections, the role of bats as a lyssavirus reservoir is well known. After discovery of bat rabies, researchers attempted to understand the pathogenesis and elucidate if differences exist between bat and carnivore rabies. Work on viruses in bats was first presented at North American Society for Bat Research (NASBR) meetings in 1973 and 1974 by Dr. Trimachi at the New York State Department of Health. He described naturally occurring rabies virus infecting big brown bats (*Eptesicus fuscus*), and the development of a micro-seroneutralization assay. The continuation of that work was published in the Journal of Wildlife Diseases a few years later (Trimarchi and Debbie 1977). The development of a sero-assay that can test low volumes of blood for rabies virus antibodies advanced future epidemiological studies in bats. Many more studies followed over the years both through natural and laboratory infections in bats. Nevertheless, the results and outcomes of these studies are difficult to assess when applying the general concepts of virology and immunology associated with other host species and viruses. Examples of this include reports of rabies virus being present in saliva of bats lacking central nervous system involvement (Pavlovich et al. 2018); high rates of rabies seroprevalence (up to 80% in some colonies) possibly due to the role of maternal antibodies conferring passive immunity (Steece and Altenbach 1989), or multiple low-dose exposures overtime through licking rather than biting (Turmelle et al. 2010). In addition, some experimental inoculations failed to produce serologic immune responses, or in some other cases, the responses were inadequate to protect against rabies virus challenge despite the presence of neutralizing antibodies (Turmelle et al. 2010). Complicating factors are that different species of bats demonstrate variable susceptibility to rabies disease and have different clinical presentations of the furious and paralytic forms. Furthermore, the difficulty of delivering a vaccine for bats (in contrast to bait vaccine targeting raccoons and foxes) and low public health awareness of bats in rabies transmission, and consequent lack of proper post-exposure treatment are some of the reasons why rabies virus transmission from bats still occur. Several surveillance studies have also indicated that bats are able to clear rabies infection with no viral transmission resulting in an antibody response, but the mechanism involved is still unclear (Kuzmin and Rupprecht 2015).

In geographic regions other than the Americas, rabies related lyssaviruses in bats exist, but rarely spill-over, constituting a low public health risk. However, it will still cause the fatal rabies-like disease and therefore precautions to avoid contact with infected saliva and appropriate pre- and post-exposure prophylaxis procedures should always be followed.

19.2.2 Paramyxoviruses

Paramyxoviruses were not recognized as important zoonotic pathogens until 1990 when Hendra and Nipah viruses emerged (Thibault et al. 2017). In bats, these viruses are usually shed in urine, which is the main route of transmission to humans and other animals causing severe neurological and respiratory symptoms with high mortality rates and no treatment. The virus has also been reported in uterine fluid as well as from partially eaten fruit, implicating other potential transmission routes involving body fluids including saliva (Chua et al. 2002). A high diversity of paramyxoviruses has been detected in bats and several have demonstrated the ability to spillover, including direct transmission from bats to humans, as well as through intermediate host species such as horses (Hendra) or pigs (Nipah). Flying foxes (*Pteropus*) have been shown to be reservoirs of Nipah and Hendra (*Henipavirus*). These viruses have reportedly been transmitted directly from bats to humans with subsequent human-to-human and nosocomial transmission (Sazzad et al. 2013) in near-annual outbreaks in Bangladesh and sporadic outbreaks in other areas.

Initially, the distribution of henipaviruses was believed to be restricted to the geographical distribution of *Pteropus* in Australia and South-East Asia. However, detections of *henipavirus*-related antibodies and nucleic acids in African fruit bats has expanded the geographical range of these viruses (Hayman et al. 2008; Drexler et al. 2009). Since these reports, numerous other surveillance studies were conducted and our understanding of the viral diversity has expanded with a number of these viruses now known to be closely related to recognized human paramyxovirus pathogens and thus are considered to be potentially zoonotic based on relatedness of genomic material. Isolations have been unsuccessful for most of these novel viruses. However, with the use of recombinant viral particles containing the attachment and fusion genes for a bat mumps virus, cross-reaction and cross-neutralization with human mumps virus was demonstrated (Katoh et al. 2016).

More than 20 viruses of this family have been isolated from bats and also identified by genetic sequences, but many remain poorly described for their epidemiology and none appear to cause mortality in bats. Some are bat viruses with no pathogenicity to other species, such as Cedar virus, whereas Tukoko virus has not been isolated and has only been characterized genetically so its pathogenicity is still unknown. Tioman and Achimota viruses were isolated from bat urine and although no human or animal disease has been reported to date, serological data from local inhabitants suggests zoonotic potential. Similarly, Mapuera virus isolated from saliva of a fruit bat in Brazil (Wang et al. 2007) has never been reported as an animal or human disease, however, it is fatal when intracranially inoculated in mice. Two other phylogenetically related viruses, one found in diseased pigs in Mexico

(Porcine rubulavirus) and another from a human case of a bat biologist returning from working in Africa (Sosuga virus) (Albariño et al. 2014) are suspected to be of bat origin due to the history and detection of the same virus in Egyptian fruit bats (*Rousettus aegyptiacus*). Various research studies, mostly targeted towards Hendra and Nipah viruses, have reported possible drivers of disease emergence including strong seasonality in excretion and correlations between bat densities, nutritional stress and various events during the reproductive season of bats (waning maternal antibodies, late pregnancy and breeding) (Plowright et al. 2014).

19.2.3 Coronaviruses

Coronaviruses belong to another well-studied viral family, many of these viruses manifest as respiratory pathogens in humans transmitted through aerosols. Bat coronaviruses are predominantly excreted in faecal material, but oral swabs (Falcón et al. 2011) and urine (Mendenhall et al. 2017) have also tested positive implicating several routes of transmission. Coronaviruses are known to frequently undergo recombination, creating new variants (Hon et al. 2008; Tao et al. 2017) that can result in spillover. Global surveillance for coronaviruses has increased significantly after SARS coronavirus emerged in China in 2002 resulting in an outbreak with 10% mortality and worldwide distribution due to global travel (Berry et al. 2015). SARS was a novel virus, not previously detected in humans, and originally palm civets and raccoon dogs were identified as the source of infection, but it later became apparent that they also develop signs of disease. The search for the potential reservoir species started, which included surveillance in bats. In 2005, serological and partial nucleic acid detection linked SARS-CoV to horseshoe bats (*Rhinolophus*) in China by identifying a closely related virus and subsequent studies identified an even larger diversity of SARS-CoV-related viruses in horseshoe bats worldwide (Hu et al. 2017; Lau et al. 2010). However, the protein responsible for recognition and attachment to host receptors (spike gene) (Lau et al. 2005; Li et al. 2005) was very diverse and none of these identified viruses could therefore be the direct source of the human SARS outbreak (Li et al. 2005). Recently, a SARS related virus using the same binding receptor as human SARS, was described (Yang et al. 2015) indicating that the virus in the horseshoe bat has the potential to infect humans directly. SARS did not emerge again after 2002, although similar sequences have been detected in bats. In 2019, a new coronavirus (SARS CoV-2) appeared causing an acute respiratory disease pandemic (COVID-19) that as of December 2020 resulted in >1,600,000 deaths worldwide. It was most similar genetically to a bat virus, but a key receptor-binding domain was nearly identical to a pangolin coronavirus (Andersen et al. 2020). Some of the first human infections of COVID-19 occurred at a seafood market in Wuhan, China that also had live animals, but no bats were sold there (Wu et al. 2020).

In 2012, Middle East Respiratory syndrome virus (MERS) was identified in the Arabian Peninsula (Zaki et al. 2012). Initially, a short nucleic acid sequence was detected in an Egyptian tomb bat (*Taphozous perforatus*) from Saudi Arabia

(Memish et al. 2013). However, it has subsequently been shown that this and other detections in bats are only distantly related to MERS and that dromedary camels are the reservoirs transmitting the virus to people. Despite the fact that MERS CoV can replicate and be shed by Jamaican fruit bats *(Artibeus jamaicensis)* in the lab (Munster et al. 2016), the ancestral origin of the virus is still unknown. Diverse coronavirus sequences were found in many different bat species worldwide leading to the hypothesis that bats host the genetic diversity of the *Alphacoronavirus* and *Betacoronavirus* mammalian-infecting genera (Woo et al. 2012).

19.2.4 Filoviruses

Filoviruses, including the Ebola (EBOV) and Marburgvirus (MARV) genera cause life threatening hemorrhagic fever in humans (Kuhn 2019) with high morbidity and mortality rates. In the last few decades, several diverse filoviruses were also detected in bats including Lloviu virus (LLOV) in Schreibers' long-fingered bats (*Miniopterus schreibersii*) in Spain and Hungary (Kemenesi et al. 2018), Mengla virus from China and Bombali virus from Sierra Leone (Goldstein et al. 2019) and Kenya.

MARV was first identified in 1967 in green monkeys imported into Europe from Uganda when laboratory workers became infected. Since then it has been detected and isolated in several African countries (Olival and Hayman 2014). Substantial evidence now exists suggesting that the Egyptian fruit bat is a reservoir of Marburg virus, without showing signs of disease (Towner et al. 2009). Longitudinal studies identified distinct viral pulses in juvenile bats that corresponded to the timing of human outbreaks, implicating birthing pulses as a driver of infection (Amman et al. 2012). Experimental infection studies of Marburg virus in captive-bred Egyptian fruit bats reported viral RNA in oral and vaginal secretions as well as excreta implicating several potential routes of transmission. However, studies have failed to demonstrate transmission indirectly through air or through direct physical contact (Amman et al. 2016; Leroy et al. 2005).

Ebolavirus was discovered in 1976 and now consists of five species including Zaire virus (EBOV), Bundibugyo (BDBV), Sudan (SUDV), Tai Forest virus (TAFV) and Reston virus (RESTV) (Kuhn 2019) all with a potentially unique ecological niche. More than 25 human outbreaks have occurred with the most significant being the 2013–2016 outbreak in Guinea, Sierra Leone and Liberia where more than 11,000 people died (Spengler et al. 2016). Index cases were reported to have had contact with dead wildlife including non-human primates and antelope; however, these species cannot be the virus reservoir since they also succumbed to the disease. Several studies reported circumstantial links of bats to Ebola virus outbreaks with no virological evidence. The only evidence published to date is partial ebolavirus RNA detected in three fruit bat species: hammer-headed bat (*Hypsignathus monstrosus*), Franquet's epauletted fruit bat (*Epomops buettikoferi*) and the little collared fruit bat (*Myonycteris torquata*). This was after an intensive study sampling bats, birds and small terrestrial vertebrates in Gabon and the Republic of the Congo (Leroy et al. 2005) and a recent report of detection in a long fingered bat in Liberia. Numerous other studies have reported the presence of *Ebolavirus* antibodies from several bat species on the African continent as well as Asia and Europe; however, this is not an indication of infection and may be representative of a closely related filovirus. The reservoir of EBOV and other ebolavirus species has yet to be identified.

Filovirus outbreaks are rare with transmission not a common event. However; if it does spillover into the human population, human-to-human transmission follows through direct contact with the body fluids of infected patients, or via contact with patient remains during traditional burial activities leading to significant public health consequences (Roddy et al. 2010).

19.2.5 Orthomyxoviruses

Orthomyxoviruses (Influenza) have segmented genomes resulting in frequent genetic reassortment events giving rise to new pandemic strains (Anon 2019). Waterfowl are considered the natural reservoirs for most influenza A virus species, whereas pigs are recognized as amplifying hosts that facilitate subsequent viral spread to humans (Garten et al. 2009). Porcine species possess receptor molecules required for viral attachment of both avian- and mammalian-specific influenza A viruses, enabling adaptation of one virus to another host through reassortment of co-infecting influenza A viruses (Ito et al. 1998).

Influenza viruses in bats have been reported from Kazakhstan (L’vov et al. 1979) and Central and South America more than 30 years later (Tong et al. 2012, 2013). The latter viruses represent unique bat-specific Influenza A viruses, resulting in the propagation of novel subtypes (H17N10 and H18N11). Although these strains are quite distant from the mammalian and avian strains described to date, the identification of a conserved region of the MHC class II as the cellular receptor used by these viruses to enter the host cells raises serious concerns (Barclay 2019). Several animal model experiments are under way to determine their pathogenesis and the threat that these strains may represent to humans and other mammals (Ciminski et al. 2019). H18N11 replicates poorly in mice and ferrets, but efficiently in bats where it is shed through feces.

More recently, surveillance in the Egyptian fruit bat in Egypt reported the detection of another influenza A virus with a bat origin from oral and rectal swabs (Kandeil et al. 2018). Analysis of the viral genome indicated that it formed a distinct lineage within the genus and was not closely related to the bat-specific influenza viruses described from the New World bats. Researchers were able to isolate the bat virus and further analysis revealed its affinity to avian-specific receptors, suggesting the virus originated from an avian H9N2 subtype. The bat population where this virus was detected was reported to be a roost in an abandoned house situated in a densely agricultural area with bats foraging in fruit trees in the village orchards (Kandeil et al. 2018), providing opportunities for virus spillover.

19.3 Bat Immunity

Many evolutionary adaptations in bats may be responsible for the large number of pathogens they have shown to harbor for prolonged periods without clinical effects. Many of these changes involve bat immune systems, which show considerable diversity among the many genera of bats; and thus, no general finding can be applied to all bats species. A thorough description of immunity in bats was reported by Baker and Zhou (2015). Briefly, bats share similar immune organs and tissue structures with other mammals (bone marrow, lymph nodes, thymus, etc.). More detailed knowledge on the function of bat immune components have been hindered by the lack of specific reagents to study their immune cells and responses. Another issue is the absence of a confirmed pathogen-free bat colony in which to study both innate and adaptive immune responses to viruses (Schountz 2014). At present, the availability of a dozen whole genome sequences of different species of bats, as well as some limited transcriptome data, has allowed a first attempt into possible adaptations that permit bat coexistence with viruses. The recently formed Bat1K genome consortium (http://www.bat1k.com) has an initial objective of chromosome-level coverage of species from each of the 21 families of bats, which will greatly facilitate the study of the co-evolution of bats and viruses (Teeling et al. 2018).

All immunoglobulin (Ig) types have been found in bats, IgM, IgA, IgG, IgE, with the exception of IgD, which has only been found in microbats. Light chains have similar structure, but the V region of the heavy chain (antigen-binding variable) shows extreme diversity. Although viral challenges have demonstrated that bats can seroconvert and produce neutralizing antibodies, in most cases responses are intriguing and not comparable to other mammals (Schountz et al. 2017). For instance, not all inoculated/vaccinated bats in the same test group will seroconvert, but at the same time, seroconversion and the presence of neutralizing antibodies is not reflective of protection against viral challenge. On the other hand, some bats can clear viruses in the absence of neutralizing antibodies suggesting other mechanisms are more important, probably the innate and maybe the cellular immune responses. For example, bats that were vaccinated and had neutralizing antibody titers for rabies were not always protected when challenged with the virus (Turmelle et al. 2010). Overall, it seems antibodies play a different and less central role in preventing viral infections in bats than in other species.

The other branch of adaptive immunity, which is predominant in viral clearance in other mammals, is the cell-mediated immune (CMI) response. At present, information on T cell populations and cytokines in bats are available mainly from genomic and transcriptomic data, where receptors and coreceptors of cytotoxic T cells (CD8+) and helper T cells (CD4+), as well as interleukin (IL) 2,4,6,10,12, TNF and IFNγ, have been confirmed. The major limitation in studying CMI responses in bats is the lack of reagents specific to bats (Banerjee et al. 2018), with only an IFNγ available for Pteropid bats. Early *in vitro* and later *in vivo* studies have reported delayed CMI responses when compared to other mammalian cells, although these remain poorly described due to the lack of reagents to identify cell types. Another stark difference in the CMI of bats may be due to their unique major histocompatibility complex (MHC) molecules. Genetic information of these surface proteins, whose main function is to bind to antigens derived from pathogens and display them on the cell surface for recognition by T-cells, is that these genes are highly contracted in bats. However, at least in *Pteropus alecto*, MHC class I has an insertion within the peptide binding groove that allows it to bind and present a broader array of peptides (Qu et al. 2019) that could counter the previous statement. Studies of the DR beta locus of MHC class II in different species of bats have suggested that roosting behavior/population size, as well as pathogen-driven selection, may reflect the differences in the capacity of various species of bats to respond to viral infections (Salmier et al. 2016).

Based on histological descriptions, most immune cells seem to be present in bats including macrophages, neutrophils, eosinophils, basophils and lymphocytes. Furthermore, B and T cells were identified in *Pteropus alecto* (Gómez Martínez et al. 2016). Of particular interest (due to the function of natural killer (NK) cells against viruses) is that an expanded and diversified KLRC/KLRD family of NK cell receptors have been described in *Rousettus aegyptiacus* (Pavlovich et al. 2018). While the amount of information available on the innate immune system of bats is relatively small, some components of the innate response seem to be conserved in at least a few species of bats. For example, the pattern recognition receptors (PRR), which include Toll-like receptors (TLRs), RIG-like receptors (RLRs) and NOD-like receptors (NLRs), are similar to other mammals to some degree. TLRs are located in the cell membrane and are involved in viral nucleic acid sensing, while RLRs are intracellular molecules that recognize viral RNAs, and NLRs are intracytoplasmic PRRs whose activation by pathogen-associated molecular patterns (PAMPs) including those of viruses, induce the production of inflammatory cytokines. Absence of inflammasome sensor genes (PYHIN) may impair or reduce the inflammatory response to viral infections, which can explain why bats may harbor some viruses with little or no pathology (Ahn et al. 2016). Interferons (IFNs) are another large family of cytokines, with group I (α, β, ω, ε, κ, τ) and III (λ), having a major role in the innate immune response to viruses. While the limited information available suggests that overall IFNs in bats function in a similar manner to other mammals, significant differences have been noted. In certain bat species, some of the IFN type I genes have been shown to be reduced in number, whereas others are expanded in comparison to mammalian species such as humans and mice. While the number of genes for IFN type III in bats are similar to that of other mammals, their expression may differ as suggested by *in vitro* experimental infection of bat immune cells. In an *in vitro* study the response of bat splenocytes to a paramyxovirus infection resulted in up-regulation of IFN type III, which may allow for the coexistence of long-term viral infection and maintenance of cell functions (Zhou et al. 2011). Differences in interferon regulatory factors (IRF) and interferon receptors may also play a role in the alternate expression patterns these cytokines may have in bats, such as IRF7 expression in *Pteropus alecto* in all tissues. This broader distribution may allow for IFN activation in more cell types than in other mammalian species. IFN type III receptors are also more widely distributed, appearing in both immune and non-immune cells with the same probable effect. Homologs to mammalian interferon stimulated genes have been found in bats, and experimental inhibition of some of these genes have resulted in viral reactivation in persistently infected cells (Strong et al. 2008).

This information only represents a few pieces of the puzzle and much remains to be determined for the proper understanding of the differences between immune responses of bats and other mammals. One of the hypotheses is that bats may asymptomatically host viruses that are pathogenic in humans by establishing tolerance to viral infections through an inhibitory immune state, rather than a strong antiviral response.

19.4 Conclusion

Bats are essential to maintain balanced ecosystems worldwide, performing diverse functions such as seed dispersal, flower pollination and pest-insect control. However, a large number of pathogens, including some viruses of public health importance have been and will continue to be detected in bats. Several of these reports are once-off detections without any follow up studies and it is not possible to make conclusions about potential risk for spillover. Bats may be a reservoir host to some of these viruses, but for most this has not been established. There are, however, studies linking bats to zoonotic events as discussed in this review. More pathogenesis studies as well as characterization of bats' immune responses are required to better understand the mechanisms involved in tolerating pathogens. In addition, the factors that can influence spillover including ecological and environmental must also be studied. Biologists, virologists, veterinarians and medical doctors should create a common interface to share data, some of which could be used for surveillance, risk assessment and a "one health" approach. Communicating information to stakeholders including the media and public should be clear, responsible and in context. High-risk behavior that increases contact with potential bat reservoirs of disease such as human population displacements, encroachment and cultural behavior (live markets or hunting and consuming wildlife), all of which increase the risk of disease spillover, should be clearly communicated. Lastly, the risk involved in handling bats and entering roosts must be acknowledged, and appropriate standard operating procedures and precautions must be followed to prevent exposure to infectious material, but also to prevent spreading of pathogens between roosts.

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Chapter 20
Bats as Hosts of Important Unicellular Endoparasites

Pablo Colunga-Salas, Giovani Hernádez-Canchola, Estefania Grostieta, and Ingeborg Becker

Abstract Some bacteria and protozoan species are important pathogens causing high mortality rates not only in humans, but also in other mammal species including bats. Infectious agents, such as viruses, bacteria, protozoa, and fungi have been reported in the order Chiroptera, but a thorough analysis of zoonotic unicellular pathogens is needed. To address this topic, we conducted an exhaustive search of literature reports on pathogenic bacterial and protozoan infections in bats, in order to summarize the current state of knowledge on these pathogens. From this search, we obtained information on seven protozoan and 12 bacterial species present in 187 bat species, which were retrieved from 169 articles. Despite all the records, bats are only considered reservoirs for two protozoan species. Thus, more studies are needed to consider bats as reservoirs for bacteria. At North American Society for Bat Research (NASBR) symposia, 17 studies have been presented and discussed, but only two focused on pathogens responsible for the principal causes of death in human populations. More worldwide studies are needed to assess the actual role of bats in public health problems and to help develop conservation measures for bat populations that need to be protected.

Keywords Bacteria · Pathogens · Protozoa · Reservoirs · Zoonosis

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20.1 Introduction

Zoonoses are diseases transmitted from animals to humans. Their importance has grown during the last century due to the increase of reported cases showing that more than 60% of infectious diseases are zoonotic (Daszak et al. 2000; WHO 2019d). The emergence of zoonotic diseases results from the complex ecological interactions between wildlife, livestock, and human populations in a rapidly changing environment (Allen et al. 2017). Given these complex interactions a new paradigm has been proposed, the *ecoepidemiology*, which addresses the interdependence between individuals and their connections with the environment [biological, physical, social and historical contexts] (Susser and Susser 1996).

Several studies propose that tropical and subtropical zones are those with the greatest risk of encountering zoonotic diseases because these areas have high biodiversity of pathogens and vertebrate hosts, including mammals (Ceballos and Ehrlich 2006; Allen et al. 2017). Bats (Chiroptera) are the second most diverse mammalian group and humans benefit from their ecological services, such as seed dispersal, flower pollination, and natural controllers of insect pests (Kasso and Balakrishnan 2013). In the Neotropics, chiropterans are one of the most diverse groups, typically representing >50% of all mammalian species (Medellín et al. 2000). Even though much is known of their biological aspects, there is a lack of information regarding the role of these mammals in the zoonotic pathogenic cycles (Mühldorfer 2013).

One of the primary evolutionary adaptations of bats is their ability to fly and, in the case of some species, travel long distances (e.g. *Tadarida brasiliensis*). This increases the possibility of infection, as well as allowing the spread of various pathogens through guano. In addition, many species are able to live in disturbed or urban areas, which allows contact between bats and human populations (Wynne and Wang 2013).

In humans, almost 90% of the infectious diseases are due to five processes including acute respiratory infections, diarrhea, tuberculosis, measles and malaria. Almost 77% of these diseases are produced by several bacterial and protozoan species (Ecker et al. 2005). Furthermore, several etiological agents of infectious diseases associated with high mortality rates in humans can also infect other mammals and provoke diseases or even death of their hosts, including bats (Mühldorfer et al. 2011a). In addition to becoming infected, mammals are also one of the most studied groups with regards to their role as possible pathogen reservoirs (Brook and Dobson 2015).

For this reason, the goal of our review is to provide an overview of the current state of knowledge on pathogenic bacterial and protozoan species recorded or isolated from bats. Specifically, the analysis was directed at documenting the important human pathogens responsible for the principal cause of death (Table 20.1) (Ecker et al. 2005). An exhaustive search in specialized databases (BioOne, Elsevier, Highwire, Iris, JSTOR, Pubmed, Scopus, SpringerLink, Wiley Online, Web of Science and Zoological Records) was done with a combination of

Table 20.1 Species of bacteria and protozoa defined as important human pathogens listed by Ecker et al. (2005) and if they have been recorded in bats

Pathogen group	Pathogen	Disease	Recorded in bats	Cause of death in bats
Bacteria	*Bordetella pertussis*	Respiratory infections, pertussis		
	Campylobacter sp.	Diarrhoeal diseases	X	
	Chlamydia trachomatis	Respiratory infections		
	Chlamydophila pneumoniae	Respiratory infections		
	Clostridium difficile	Diarrhoeal diseases	X	
	Clostridium tetani	Tetanus		
	Escherichia coli	Diarrhoeal diseases	X	
	Haemophilus influenzae	Respiratory infections, bacterial meningitis, otitis media	X	
	Listeria monocytogenes	Diarrhoeal diseases	X	
	Moraxella catarrhalis	Otitis media		
	Mycobacterium tuberculosis	Tuberculosis	X	
	Mycoplasma pneumoniae	Respiratory infections		
	Neisseria meningitidis	Bacterial meningitis		
	Salmonella sp.	Diarrhoeal diseases	X	
	Shigella dysenteriae		X	
	Staphylococcus aureus	Respiratory infections	X	X
	Streptococcus pneumoniae	Respiratory infections, bacterial meningitis, otitis media	X	X
	Streptococcus pyogenes	Otitis media		
	Treponema pallidum	Syphilis		
	Vibrio cholerae	Diarrhoeal diseases		

(continued)

Table 20.1 (continued)

Pathogen group	Pathogen	Disease	Recorded in bats	Cause of death in bats
Protozoa	*Cryptosporidium parvum*	Diarrhoeal diseases	X	
	Cyclospora cayetanensis			
	Encephalitozoon intestinalis			
	Entamoeba histolytica			
	Giardia sp.		X	
	Leishmaina shawi	Leishmaniasis		
	Leishmania braziliensis		X	
	Leishmania chagasi		X	
	Leishmania colombiensis			
	Leishmania donovani			
	Leishmania garnhami			
	Leishmania guyanensis			
	Leishmania lainsoni			
	Leishmania major		X	
	Leishmania mexicana		X	
	Leishmania naiffi			
	Leishmania panamensis			
	Leishmania peruviana			
	Leishmania pifanoi			
	Leishmania tropica		X	
	Plasmodium falciparum	Malaria		
	Plasmodium vivax			
	Trypanosoma brucei	Trypanosomiasis		
	Trypanosoma cruzi	Chagas disease	X	

several key words including pathogen species, “bat*”, “chiroptera*”, “morcego*”, and “murciélago*” to answer the following questions: (1) What is the current state of general knowledge on pathogens associated with bats? (2) Which pathogens have been recorded in bats worldwide? (3) Can bats be considered reservoirs of these pathogens? and (4) What has been the importance of the North American Society for Bat Research (NASBR) in the generation and communication of this type of work during its 50 years of scientific meetings?

20.2 Advances in the Study of Bacteria and Protozoa Associated with Bats

To date, 187 bat species in 15 families are considered hosts of 19 unicellular parasite species (seven protozoan species and 12 bacterial species, Table 20.1; Supplemental Material) causing several infections and diseases (Colunga-Salas et al. 2019). A total of 169 articles in which unicellular pathogens were registered in bats have been published so far, and these unicellular pathogens have been recorded in 40 countries (Figs. 20.1a and 20.2a). Brazil, and the United States lead the global scientific investigation of pathogens in bats with 85 papers based on the author’s affiliations. The high number of studies from Brazil are due to the importance of *Trypanosoma cruzi*, the etiological agent of Chagas disease, as well as the association of this protozoan with bats.

Phyllostomidae is the most studied bat family with a total of 366 records (305 bacteria records and 61 records for protozoa). This family is endemic to the Neotropics and distributed from Mexico to the Caribbean, Central America and South America. The vespertilionid, pteropodid and molossid bat families are the next most studied with 98, 76, and 65 total records, respectively. Differences in the number of records for each family may be due to the fact that Phyllostomidae has the highest species richness in the Neotropics (Clare et al. 2007), where many of these studies have been done. The most studied bat family in the Old World is Vespertilionidae, where this family is likely originated (Lack and Van Den Bussche 2010). These four bat families are the most studied for other pathogens such as viruses due to their high species richness and better known biological patterns (Wong et al. 2007).

Considering only protozoan pathogens, 97 published works have been reported in 14 countries (Fig. 20.1). The most productive countries according to author affiliation were Brazil, Colombia, United States, and United Kingdom with a total of 53, 12, 11, and 10 published articles, respectively.

The network of collaborations was analyzed using Vantage Point V.12 software. For protozoa, collaborations involved 24 countries and the five with the highest degree of networks in decreasing order are Brazil, United States, Ecuador, United Kingdom and Czech Republic (Fig. 20.1b). Worldwide, the most important collaborations (in terms of the number of affiliations per article) occurred between Spain-Australia and Israel-Ethiopia (Fig. 20.1b). In general, most of the published

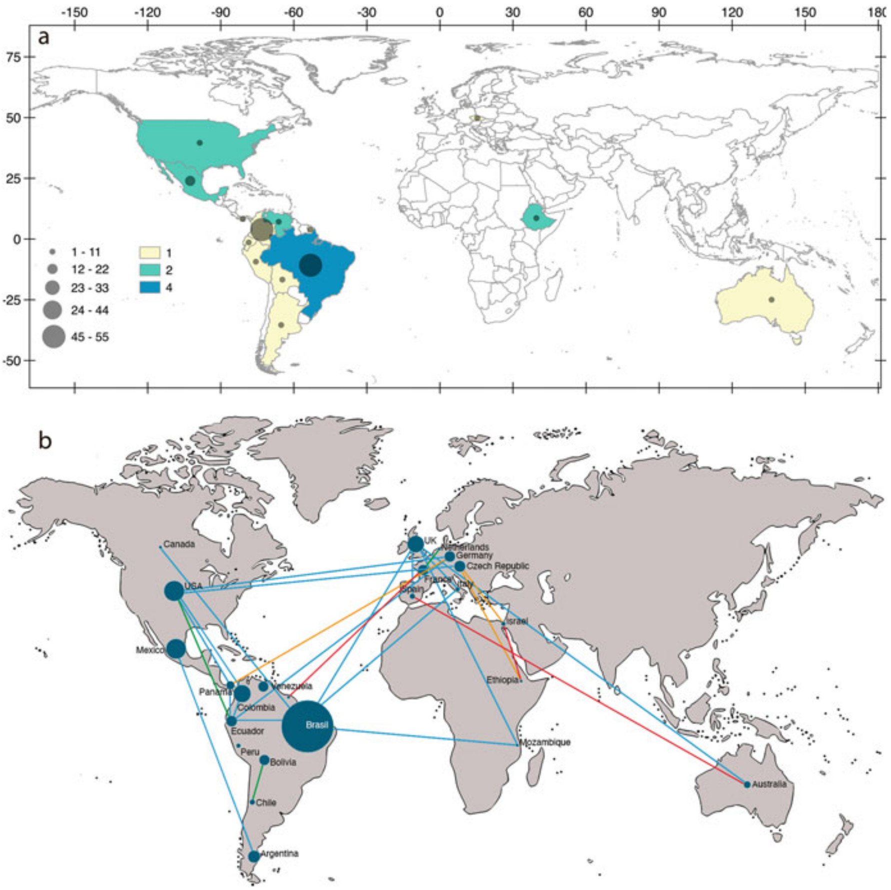

Fig. 20.1 Studies of protozoa pathogens in bat species worldwide. (**a**) Distribution map of protozoan species associated with bats. Circle size represents the number of bat species analyzed in each country. Color intensity of countries corresponds to the number of protozoan species detected. (**b**) Global collaboration network among countries for protozoan pathogen species detection. Circle size represents the number of author affiliations by country. Cross-correlation indexes are shown by line color, blue = <0.25, green = 0.25 – 0.5, yellow = 0.5 – 0.75, red = >0.75

works have been done in Latin American countries, with many collaborations among themselves and with European countries (Fig. 20.1b).

Concerning bacterial pathogens, a total of 72 articles conducted in 29 countries were found (Fig. 20.2). The global network of collaboration was composed of 31 countries, of which the five most productive in descending order are the United States, Germany, Malaysia, Australia, and Brazil with 17, 12, 7, 6, and 5 published articles, respectively (Fig. 20.2b).

Despite the number of published works on bacterial pathogens associated with bats (72 articles) and the number of countries where research was conducted, the

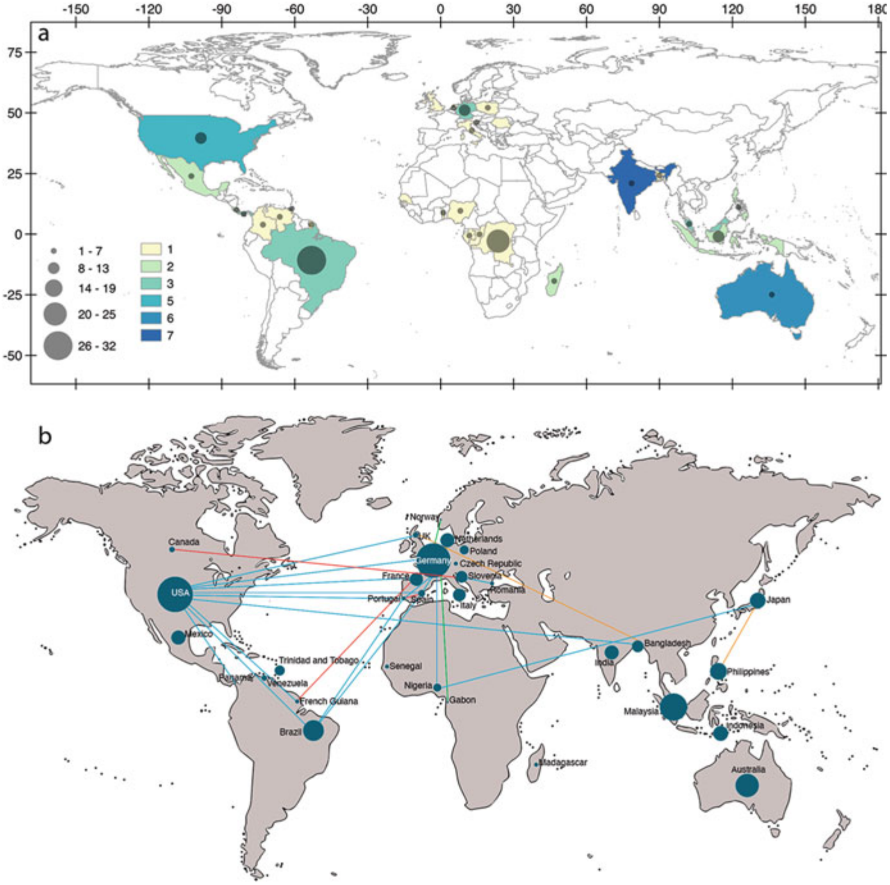

Fig. 20.2 Studies of bacterial pathogens in bat species worldwide. (**a**) Distribution map of bacterial species associated with bats. Circle size represents the number of bat species analyzed in each country. Color intensity of countries corresponds to the number of bacterial species detected. (**b**) Global collaboration network among countries for bacterial pathogen species detection. Circle size represents the number of author affiliations by country. Cross-correlation indexes are shown by line color, blue = <0.25, green = 0.25 – 0.5, yellow = 0.5 – 0.75, red = >0.75

collaboration network is not intricate because in most papers the author affiliations correspond to the country of origin of the sampled bats (Fig. 20.2b). This lack of collaboration potentially demonstrates the interest of research in bacterial pathogens that represents a public health problem in their own countries [e.g. enteropathogens in Malaysia (Lee and Puthucheary 2002), Australia (Ferrah et al. 2016), Germany (Bozorgmehr et al. 2017), and India (Saha et al. 2019)].

The initial detection method of unicellular pathogens was by microscopy and/or culture. Detection methods gradually changed to serological tests, then to molecular tests and more recently to Next Generation Sequencing (NGS) (Colunga-Salas et al. 2019). The principal detection methods used to date are by isolation, which was used in 117 articles, followed by molecular biological (64), biochemical (51), microscopy (48), serological (13), xenodiagnostic (12), and histopathological examination (2). Only xenodiagnostic tests were used for detection of *T. cruzi* (Schenone 1999). However, it is important to note that not all serological tests are indicative due to unspecific or cross-reaction of antibodies with other pathogens, even among different pathogen families. For this reason, molecular tests for confirming infections are mostly used today (Colunga-Salas et al. 2020).

Geographically, 99% of all protozoan records (447/450; Colunga-Salas et al. 2019) associated with bats have been made in the Americas, whereas the remaining were registered in Europe, Africa, and Australia, with one record each (Fig. 20.1a). The bacteria records are more widespread throughout the world (Fig. 20.2a), with the highest density of records in the Americas (97/243 = 40%), followed by Africa (20%), Asia (18%), Europe (17%), and Oceania (5%). However, the tropics are the most studied areas in terms of analyzed bat species, as compared to temperate areas (Fig. 20.2a).

20.2.1 Respiratory Infection and Bacterial Meningitis

The pathogen species causing respiratory and meningitis infections that are associated with bats include *Staphylococcus aureus*, *Haemophilus influenzae*, and *Streptococcus pneumoniae* (e.g. Henry et al. 2018; Olatimehin et al. 2018). Most of the studies are based on isolation, microscopy and/or biochemical factors (Colunga-Salas et al. 2019).

Staphylococcus aureus is a highly adaptable and dangerous commensal bacterium that colonizes skin surfaces, mainly nares, axillae, vagina, and pharynx in humans, representing an important public health concern (Chambers 2001). One of the important findings related to this species is that drug-resistant strains, which can cause treatment problems, have been documented in humans (Chambers 2001) and bats (Walther et al. 2008). Chiropterans are the most studied host within mammals with at least one record per continent and a total of 27 papers. In all articles, with the exception of one (Richman et al. 1982), the detection of this bacterium was carried out by isolation and/or biochemical features, and eight studies were confirmed by molecular techniques (Colunga-Salas et al. 2019).

Haemophilus influenzae has been isolated only from fecal samples of seemingly healthy grey-headed flying foxes (*Pteropus poliocephalus*), collected after natural defecation from a colony in Australia (Henry et al. 2018). The final identification of this bacterium was done with Next Generation Sequencing analysis (NGS). As with *S. aureus*, *H. influenzae* is a common commensal bacterium that can cause pneumonia and meningitis (Whittaker et al. 2017). This bacterium has been previously isolated from fecal samples of children with diarrhea in France (Mégraud et al. 1988). The authors suspect that *H. influenzae* found in the gastrointestinal tract could have originated in the oropharynx and saliva, which could be the same infection route for bats during feeding. The main contagious form is transmitted through respiratory droplets (CDC 2019c), however, more studies must be done in order to establish the species of wild mammals that act as hosts and potential reservoirs.

As with *H. influenzae, S. pneumoniae* has been only recorded in pteropodid bats (Colunga-Salas et al. 2019). An Asian record was first isolated in culture media from fecal samples of Leschenault's rousette bat (*Rousettus leschenaultii*) in India and identified by NGS analyses. An American record is from two Wahlberg's epauleted fruit bats (*Epomophorus wahlbergi*) in the Oregon Zoo, USA (Helmick et al. 2004), where the detection of the bacterium was made from pharyngeal culture screening. This bacterium is transmitted through droplets from person to person or by contact with contaminated surfaces, and causes pneumonia or meningitis in mammals, including humans (Corless et al. 2001).

Only *S. aureus* and *S. pneumoniae* have been associated with fatal reports due to a respiratory infection by bacteria in bats, Nathusius' pipistrelle (*Pipistrellus nathusii*) and the common noctule (*Nyctalus noctula*), which result in severe interstitial pneumonia (Mühldorfer et al. 2011b). In the case of a gravid *E. wahlbergi*, the cause of death was attributed to bronchopneumonia caused by *S. pneumoniae* (Helmick et al. 2004). These reports indicate that bats are susceptible to these respiratory infections as has been previously demonstrated (Cogswell-Hawkinson et al. 2012).

20.2.2 Diarrheal Diseases

Of the pathogens associated with diarrheal diseases, enteropathogens are commonly found in bats (Colunga-Salas et al. 2019). The vast majority of these food-borne pathogens are regarded as the normal gastrointestinal bacteria flora of bats, such as *Escherichia coli*, *Salmonella* sp., *Shigella dysenteriae*, and *Campylobacter jejuni*, or associated with severe intestinal pathogens such as *Listeria monocytogenes*, *Giardia* sp., and *Cryptosporodium parvum* (Ecker et al. 2005).

The food-borne bacteria *E. coli* is the principal cause of death due to diarrheal diseases in children <5 years throughout the world (Lanata et al. 2013) and also is the most detected bacterium in bats. Phyllostomids, endemic to the Neotropics, are the most studied bat family for *E. coli* infections. Pteropodid and vespertilionid bats are the second and third most studied families (Fig. 20.2a). *Escherichia coli* infection is acquired through the intake of contaminated food, including fruits (Beuchat 2002), which represents a probable source of infection for frugivorous species. Under certain circumstances, this bacterium has been associated with some gastrointestinal and urinary infections in bats (Mühldorfer et al. 2011b) making them susceptible to *E. coli* infections (Mühldorfer 2013).

As with *E. coli*, *Salmonella* is considered part of the normal intestinal flora of both humans and bats (Mühldorfer 2013), but in the case of susceptible individuals, this bacterial genus can cause diseases in both. Only two species are recorded in bats, *Salmonella enterica* (serovar Typhimurium, Anatum, San Diego, Llandoff, Enterica, Blockley), and *Salmonella bongori*, both of which have been detected in tissues and feces on all continents, mainly by isolation but some cases were confirmed by molecular techniques, including NGS analyses. Of these species and serovars, *S. enterica* Enterica and *S. enterica* Typhimurium are mainly associated with human and animal diseases (Mühldorfer 2013). The bat family most studied is Pteropodidae from the Old World, followed by Molossidae and Phyllostomidae with eight records in the Americas. The majority of bat species in which this bacterial genus has been recorded are frugivorous (Colunga-Salas et al. 2019).

Shigella dysenteriae, a highly contagious bacterium obtained from feces of *Pteropus poliocephalus* and detected by NGS analyses, has only been recorded once in bats (Henry et al. 2018). This bacterium is mainly transmitted by contact of fluids on contaminated surfaces or by sexual transmission causing Shigellosis, whose main symptoms in humans are gastroenteritis or severe dysentery (CDC 2019b).

The last bacterium of this infection group, *Campylobacter jejuni*, has been isolated from feces of pteropodid bats from Asia. However, other authors have recorded unspecified *Campylobacter* species from European vespertilionid bats (Hazeleger et al. 2018). Although the main infection route of *Campylobacter* is by contaminated food, some arthropods can be infected and probably transmit this bacterium (Hald et al. 2008). These can be possible infection routes because some infected bats are frugivorous or nectarivorous (Pteropodidae) and insectivorous (Vespertilionidae).

Only one study reported antibiotic resistant enteric bacteria strains in bats, which correspond to strains of *E. coli* and *Salmonella* from phyllostomid, molossid, and vespertilionid species from Brazil (Cláudio et al. 2018). This finding provides evidence that humans and bats coexist closely in their environments, which favors the dispersion and possible inter-specific transmission of pathogens.

For protozoans, only two taxa have been recorded in bats, *Giardia* sp. and *Cryptosporidium parvum*. The first taxon was detected in fecal samples of *Molossus molossus* and *Noctilio albiventris* in Brazil, whereas *C. parvum* was found in vespertilionid bats from America, Australia, and Europe (Colunga-Salas et al. 2019). Both protozoa species are mainly transmitted by drinking contaminated water, where the infective phase of both protozoa is found, causing diarrheal infections or extraintestinal cryptosporidiosis infections (CDC 2019a).

20.2.3 Tuberculosis (TB)

Mycobacterium tuberculosis is the only representative species of the tuberculosis group (TB) found in bats according to Ecker et al. (2005). Only three positive records exist for this bacterium in bats from India (*Pteropus medius* and *Rousettus leschenaultii*) and the United States (*Tadarida brasiliensis*) (Colunga-Salas et al. 2019). In these bats, the bacterium was isolated from the individuals and/or fecal samples. This air-borne pathogen usually affects the lungs but can also attack any part of the body such as the kidneys, spine, and brain. Not everyone infected with TB becomes sick, but without treatment, latent tuberculosis can progress to disease, which can be fatal (CDC 2019c). However, hepatotoxicity and clinical hepatitis are serious adverse effects associated with drugs that are currently used for the treatment of tuberculosis (Getahun et al. 2015). The only bat in which this pathogen has been reported to cause death due to severe thoracic tuberculosis is the Indian flying fox, *P. medius*, from India (Griffith 1928).

20.2.4 Leishmaniasis

Leishmaniasis is an important protozoan disease caused by several species in the genus *Leishmania* (Lozano-Sardaneta et al. 2018). The main risk areas are the tropics throughout the world, but mainly in South America, North Africa, and the Middle East (WHO 2019a). These vector-borne protozoans are transmitted by dipterans of the sandfly genus *Phlebotomus* in the Old World, and *Lutzomyia* in the New World (Akhoundi et al. 2016). Several mammalian species have been described as reservoirs of this genus, of which dogs, opossums, and bats are the more important (Quinnell and Courtenay 2009).

To date, 24 species of bats from six families have been recorded as hosts and potential reservoirs of the genus *Leishmania*, with a total of 52 records retrieved from 11 articles (Colunga-Salas et al. 2019). A total of five species of *Leishmania* have been recorded in bats: *Leishmania braziliensis*, *Leishmania infantum/chagasi*, *Leishmania major*, *Leishmania mexicana*, and *Leishmania tropica*. From these species, only *L. infantum/chagasi* is attributed to visceral leishmaniasis, also known as kala-azar, which is fatal if left untreated in over 95% of cases (WHO 2019a). This species has been detected in the Americas mainly from phyllostomid bats.

Cutaneous leishmaniasis, which is the most common form of leishmaniasis leading to skin lesions (mainly ulcers), is caused by *L. braziliensis*, *L. major*, *L. mexicana*, and *L. tropica*. These species are commonly recorded in bats, mainly in the Americas, with only one record in Africa (Kassahun et al. 2015). Of these four species, *L. mexicana* is the most studied, with 25 records mainly from Phyllostomidae (Colunga-Salas et al. 2019). All records from these species of *Leishmania* are cutaneous and mucocutaneous leishmaniasis from Brazil, Ethiopia, and Mexico (WHO 2019a).

Unlike the other pathogens analyzed in this review, the detection of *Leishmania* has been done by molecular methods in all the studies, except one that used a serological immunofluorescence antibody test (IFAT) and validated with a PCR method (Savani et al. 2010). Additionally, real-time PCR (qPCR) was used in four studies to detect *Leishmania* in bats, thereby achieving confirmatory records and enabling parasite counts in bats (Medkour et al. 2019).

Sandflies preferentially choose rich organic moist soil or contaminated soil as shelters (Feliciangeli 2004). There are reports of phlebotomines inhabiting caves with bats (Polseela et al. 2007), which may provide blood as a food source for the females of the genera *Lutzomyia* and *Sergentomyia* (Alves et al. 2008). *Lutzomyia vespertilionis* shows a distinct preference for bats (Christensen and Herrer 1980) and has been proposed as a potential vector of trypanosomatids associated with bats (Christensen and Herrer 1975). However, more studies are needed in order to confirm whether other phlebotomine species act as *Leishmania* vectors in bats.

20.2.5 Chagas Disease

Chagas disease, or American trypanosomiasis, is an illness whose chronic stage is characterized by the colonization of the heart and digestive muscles by the parasite, *Trypanosoma cruzi* (WHO 2019b). Despite some cases reported in Europe (Gascon et al. 2010), the origin of this disease is in the Americas, with most reports in Latin America, from where it spread by human migrations to other parts of the world (Rassi and Marin-Neto 2010). This vector-borne disease is transmitted by contact with infected blood-sucking triatomine bugs, including incidental intake of the vector or contaminated food (Shikanai-Yasuda and Carvalho 2012). The current knowledge on *T. cruzi* infection in bats is the most comprehensive compared to other pathogens, with 81 published studies in 90 New World bat species. The records are distributed from the United States to Argentina (Colunga-Salas et al. 2019). Phyllostomids are by far the most studied family of bats for *T. cruzi* infections, probably since this family is the most specious in America (Clare et al. 2007). The genus *Phyllostomus* has the largest number of records of infections by *T. cruzi* reported for a bat.

The study of this protozoan in bats dates back to 1932, when four phyllostomid species where found to be positive after testing blood samples by microscopy methods (Clark and Dunn 1932). Microscopy, isolation, and PCR currently are the most used detection tests (Colunga-Salas et al. 2019). The possible infection route of *T. cruzi* in bats is by eating contaminated food or insects, since most of the positively tested bat species are frugivorous and insectivorous, and evidence suggests that ingestion of contaminated fruits can lead to infections by *T. cruzi* (Shikanai-Yasuda and Carvalho 2012).

20.3 Implications of Bats as Reservoirs of Unicellular Pathogens

Many definitions of *reservoir* have been proposed, some of which are contradictory to each other, which creates confusion. However, some authors proposed that a reservoir must be demarcated as one or more epidemiologically connected populations or environments in which a pathogen can be maintained and from which the infection is transmitted to the defined target population (Haydon et al. 2002).

Bats have been considered reservoirs of many pathogens, without sufficient evidence. Some of the pathogens evaluated in this chapter can be transmitted orally or by contact with contaminated water, mainly affecting people in poor areas lacking primary health services (WHO 2019c). Likewise, bats that inhabit urban and rural ecosystems, can acquire microorganisms from insect and environmental sources and thereby serve as a reservoir of several pathogens. While many studies are focused on pathogen prevalence in wildlife, information on bats is limited (Mühldorfer 2013).

Regarding the protozoan pathogens analyzed in this chapter, bats have been considered reservoirs only for *Leishmania* and *Trypanosoma* parasites (Rassi and Marin-Neto 2010). For other protozoan pathogens, such as *Cryptosporodium parvum* and *Giardia* sp., more studies on bat species are required, since no conclusive information is currently available. In the particular case of *C. parvum*, reservoirs must shed oocysts into the environment to perpetuate the infection (Mosier and Oberst 2006), but in bats no confirmatory evidence of these infective structures have been found. In *Giardia*, the infectious cyst must be released from the bat, yet the only work on giardiasis done in Chiroptera does not report this stage (Santana-Lima et al. 2018).

To consider bats as reservoirs of bacterial pathogens is complex. Food-borne bacterial species, some of which are beneficial intestinal flora of some mammals, can be shed by bats into the ecosystem and become an infection source for other animals, including humans (Adesiyun et al. 2009). For *S. aureus* and *S. pneumoniae*, more studies need to be done in order to establish whether bats are reservoirs of these bacterial pathogens, since current evidence suggests that bats are susceptible to fatal respiratory infections caused by them (Mühldorfer 2013).

The role of bats as reservoirs of globally important unicellular pathogens remains open and uncertain. Their incrimination is a complicated decision due to the lack of confirmatory evidence. The presence of some pathogens (*Giardia, C. parvum*, *H. influenzae*, *L. monocytogenes*, *S. dysenteriae* and *S. pneumoniae*) in bats is restricted only to a few particular regions of the world and in some cases their presence does prove their role as reservoirs in other mammalian species. Therefore, bats can be considered reservoirs only for *Leishmania* and *Trypanosoma* parasites, which cause diseases with much lower global death rates per year as compared to other unicellular pathogens responsible for respiratory or diarrheal infections, such as tuberculosis, malaria, tetanus, pertussis, syphilis and bacterial meningitis (Ecker et al. 2005). Currently available information remains unclear whether bats play any role in the infection cycles of these pathogens, and more effort is needed to reduce the mortality of all these diseases worldwide.

In many cases, bats are not involved in the spread of disease, but regretfully become victims of disease control efforts. There is evidence that the use of DDT and other organophosphorus insecticides to control malaria and *Leishmania* vectors in Jordan have led to a decline in population densities of the Egyptian fruit bat (Amr et al. 2006). Thus, the correct use of the term *reservoir*, and the monitored and planned implementation of pest control strategies must be carried out with great responsibility, as they can have negative effects on bat populations and the valuable ecosystem services they provide.

20.4 Presentations at NASBR Meetings

Some works on unicellular endoparasites have been presented in previous NASBR meetings, including 17 studies since its first meeting in 1970 (Table 20.2). However, only three presentations specify the bacteria or protozoa species detected, and just two include parasite species listed by Ecker et al. (2005), *Leishmania* in Mexican bats and malaria.

The first NASBR meeting presentation on bacteria or protozoa was at Madison, Wisconsin in 1999. It was a poster focused on describing the oral microbiota of bats by Desoto et al. at Interamerican University of Puerto Rico. Since then, other studies were presented in 2006, 2012, 2013, 2017, and 2018. In total, 11 studies focusing on bacteria and six on protozoa have been submitted (Table 20.2). The year in which most studies were presented was in 2013 and 2018, with five presentations each (Fig. 20.3).

Considering only bacteria studies, some of them have been focused on microbiota from the gut or intestinal tract of several bat species (Desoto in 1999; Clem in 2006; Hoyt in 2013; Duncan in 2017; Galey in 2018; Gaona in 2018; Ingala in 2018; Table 20.2). Molecular methods have been used, including three by the amplification of 16S rDNA genes (Duncan in 2017; Galey in 2018; Gaona in 2018) and one used NGS analyses (Hoyt in 2013). The use of NGS for the study of the microbiomes can be extended to the sampling of some pathogenic bacteria in bats from fecal samples, which are less invasive than traditional methods (Boston et al. 2012; Walker et al. 2016). The use of this type of molecular method more easily detects a greater amount of bacterial species than other methods, as is the case of the only records of *H. influenzae* and *S. dysenteriae* from the feces of bats (Henry et al. 2018).

Despite the importance of some species of bacteria and protozoa to public health and for causing disease and death in bats, the importance of the NASBR meetings on the studies of these pathogens has just begun. The inclusion of unicellular

Table 20.2 Studies presented in previous NASBR symposia on unicellular endoparasites of bats

NASBR meeting	Protozoa	Bacteria
Madison, Wisconsin, USA, 1999	Desoto et al.	–
Wilmington, North Carolina, USA, 2006	–	Kennard et al.
		Clem et al.
San Juan, Puerto Rico, 2012	Courtney and Vonhof	Courtney and Vonhof
San José, Costa Rica, 2013	Aparecido-Márquez	Aparecido-Márquez
	Gutiérrez-Granados	Hoyt
	Christe	
Knoxville, Tennessee, USA, 2017	Beltz	Duncan et al.
		Kelly et al.
Puerto Vallarta, Jalisco, Mexico, 2018	Cuéllar-Torres et al.	Colunga-Salas et al.
		Galey et al.
		Gaona et al.
		Ingala et al.

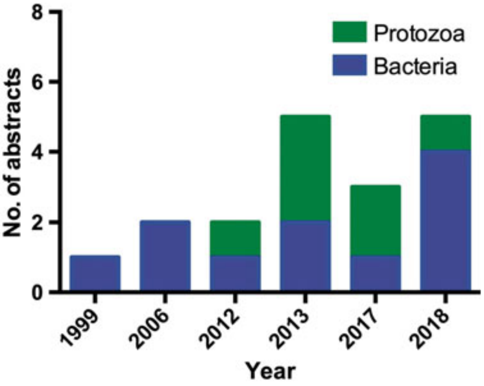

Fig. 20.3 Studies on bacteria and protozoa presented in North American Society for Bat Research (NASBR) symposia

endoparasite research in the scientific community must be strengthened because this symposium has proven to be an excellent way for these important works to become known and hopefully cause an impact on public and veterinary health. It is imperative to carefully establish whether bats can be considered reservoirs of specific pathogens and thereby avoid their unjustified stigmatization.

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Chapter 21
Bats, Bat Flies, and Fungi: Exploring Uncharted Waters

Danny Haelewaters, Carl W. Dick, Kristel Paola Cocherán Pittí, Katharina Dittmar, and Bruce D. Patterson

Abstract Bats serve as hosts to many lineages of arthropods, of which the blood-sucking bat flies (Nycteribiidae and Streblidae) are the most conspicuous. Bat flies can in turn be parasitized by Laboulbeniales fungi, which are biotrophs of arthropods. This is a second level of parasitism, hyperparasitism, a severely understudied phenomenon. Four genera of Laboulbeniales are known to occur on bat flies, *Arthrorhynchus* on Nycteribiidae in the Eastern Hemisphere, *Dimeromyces* on Old World Streblidae, *Gloeandromyces* on New World Streblidae, and *Nycteromyces* on Streblidae in both hemispheres. In this chapter, we introduce the different partners of the tripartite interaction and discuss their species diversity, ecology, and patterns of specificity. We cover parasite prevalence of Laboulbeniales fungi on bat flies, climatic effects on parasitism of bat flies, and coevolutionary patterns. One of the most important questions in this tripartite system is whether habitat has an influence on parasitism of bat flies by Laboulbeniales fungi. We hypothesize that habitat disturbance causes parasite prevalence to increase, in line with the "dilution effect."

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This can only be resolved based on large, non-biased datasets. To obtain these, we stress the importance of multitrophic field expeditions and international collaborations.

Keywords Ectoparasitic fungi · Fieldwork · Hippoboscoidea · Hyperparasites · Multitrophic interactions · Parasitism

21.1 Parasites and Parasites of Parasites

Of the traditional categories of ecological relationships, parasitism is arguably the most common in nature. Price (1980) began his *Evolutionary Biology of Parasites* by arguing that "[it] has not been generally realized that the most extraordinary adaptive radiations on the earth have been among parasitic organisms." A decade later, Windsor (1990, 1995) made a case to give *equal rights* to parasites, as they may equal in number free-living species (Price 1980; Windsor 1998). Indeed, interactions among trophic levels may be an important driver of microevolutionary processes ultimately leading to reproductive isolation and thus speciation. Although parasites maintain the stability, integrity, and structure of ecosystems and are important contributors to ecosystem functioning (Brooks and Hoberg 2001; Hudson 2005; Frainer et al. 2018), studies on species diversity that include parasites are rare (Wibbelt et al. 2009; Carlson et al. 2020).

Taking it one step further, *hyperparasitism* (parasitism of other parasites) is also thought to be a common phenomenon (Parratt and Laine 2016). When we suggest that parasites are a legitimate part of the earth's biodiversity and important components of ecosystems, this applies to hyperparasites as well; all organisms are almost sure to pick up a parasite during their lifetime, even parasites. Hyperparasitism is relatively common. For example: entire aggregations of myialgine mites can be attached to and feed on the hemolymph of bloodsucking hippoboscoid flies (Goater et al. 2018), parasitic wasps can be parasitized by other wasps (van Nouhuys et al. 2016), and ectoparasitic bat flies are prone to carrying ectoparasitic fungi (Haelewaters et al. 2018b). Although common, hyperparasites are often overlooked. As a result, virtually nothing is known regarding functional roles and key ecological and physiological interactions between hosts and their (hyper)parasites.

21.2 The Vampire's Vampire

As a remarkably successful mammalian radiation, bats (Order Chiroptera) have become hosts to numerous groups of parasites and pathogens. Their ecological abundance and sometimes dense roosting aggregations in combination with high roost fidelity create conditions favorable for transmission of symbionts. There are nearly a million described insect species on Earth (Grimaldi and Engel 2005) and many vertebrates are infested by parasites. However, true ectoparasites—blood feeders that spend most of their life-span on the host—are reported in only four orders (Diptera, Hemiptera, Phthiraptera, and Siphonaptera) and all but the Phthiraptera contain clades that have radiated on bats. Bat flies, with about 570 nominal species, have far surpassed the bat fleas (Ischnopsyllidae, 122 species), and bat bugs (Polyctenidae, 32 species) in species richness.

Bat flies have traditionally been divided into two families (Streblidae and Nycteribiidae) and together with tse tse (Glossinidae) and keds/louse flies (Hippoboscidae) form the superfamily Hippoboscoidea (Petersen et al. 2007). The Hippoboscoidea, as well as the bat flies (Streblidae+Nycteribiidae), have generally been accepted as monophyletic (Dittmar et al. 2006; Petersen et al. 2007). Moreover, there is support for a monophyletic Nycteribiidae, but not for the family Streblidae as currently comprised (Dittmar et al. 2015). All bat flies are obligate blood feeders and they are found only in association with bats. The streblids reach their zenith of diversity in the New World tropics, particularly in association with the Phyllostomidae. For example, about 80% of the described genera and 70% of the described species of Streblidae are known from the tropics and subtropics of South and Central America, including tropical portions of Mexico (Dick and Patterson 2006).

21.2.1 Nycteribiidae

The Nycteribiidae family is represented by 276 recognized species, arranged into 11 genera and three subfamilies. These flies are often referred to as “spider flies” due to the dorsal attachment of the legs, giving them a superficial “spider-like” appearance (Fig. 21.2a). The subfamilies and genera are largely similar in overall morphology, and appear to vary more along a gradient of size rather than shape. All nycteribiid species are entirely wingless, yet still possess halteres. Their global distribution is largely tropical and subtropical, but nearly 80% of nycteribiid species are limited to the Eastern Hemisphere. In the Western Hemisphere, nycteribiids mainly parasitize species of the Vespertilionidae, but also the Thyropteridae and one genus of Phyllostomidae (*Gardnerycteris*).

21.2.2 Streblidae

Streblidae is represented by 240 recognized species, arranged into 33 genera and five subfamilies. Similar to nycteribiids, this family possesses much size variation, ranging from the tiny *Mastoptera minuta* (total length 0.5 mm) to the large *Joblingia schmidti* (total length 5.5 mm). However, within this family there exists much shape variation (Figs. 21.2b–f), including laterally-compressed “flea-like” forms (e.g.,

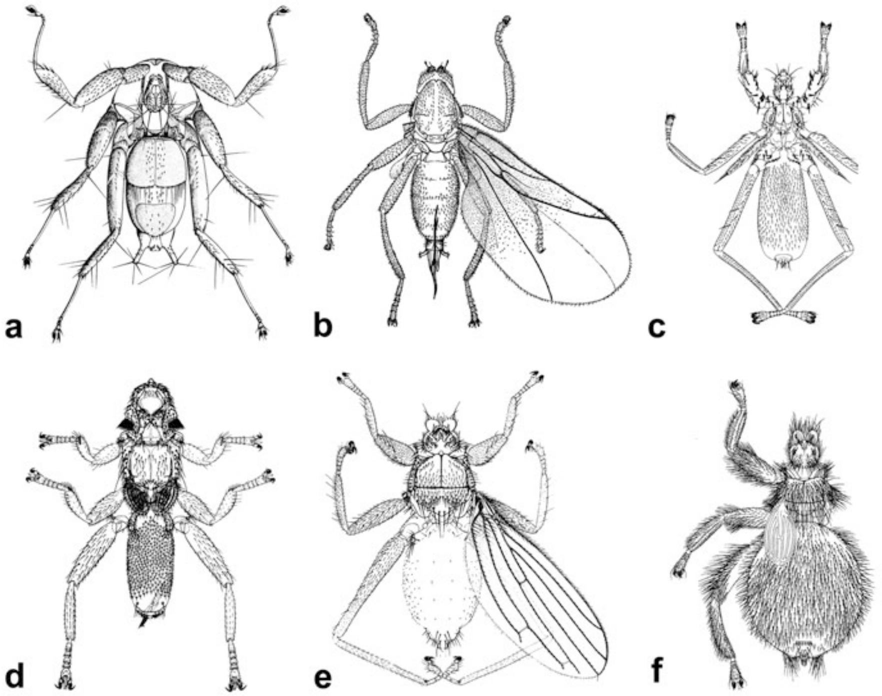

Fig. 21.1 Dorsal habitus drawings of six species of bat flies, depicting some of the morphological diversity present in the group. (**a**) Nycteribiidae: *Phthiridium biarticulatum* (Hermann), female, modified from Theodor (1967). (**b**)–(**f**) Streblidae, (**b**) *Ascodipteron africanum* Jobling, male, modified from Jobling (1940). (**c**) *Neotrichobius stenopterus* Wenzel and Aitken, female, from Wenzel et al. (1966). (**d**) *Metelasmus pseudopterus* Coquillett, male, modified from Jobling (1936). (**e**) *Speiseria ambigua* Kessell, female, modified from Jobling (1939). (**f**) *Anatrichobius scorzai* Wenzel, female, from Wenzel et al. (1966)

Nycterophiliinae), dorso-ventrally compressed forms (e.g., Streblinae), dealate and endoparasitic forms (e.g., Ascodipterinae), forms with extremely elongated legs (e.g., some Trichobiinae), and also flies that possess the typical muscoid form (e.g., some Trichobiinae). The streblids are far more diverse in the tropics and subtropics of the Western Hemisphere, which possesses 67% of the species diversity. There, the Streblidae have diversified extensively with phyllostomid and mormoopid bats, but also parasitize members of the Emballonuridae, Furipteridae, Molossidae, Natalidae, Noctilionidae, and Vespertilionidae.

21.2.3 Host Specificity

Host specificity is one of the most intriguing properties to emerge from host-parasite associations. It is a measure of the degree to which a parasite species occurs on a

Fig. 21.2 A *Penicillidia conspicua* bat fly (Nycteribiidae) collected from a *Myotis daubentonii* bat, heavily parasitized by *Arthrorhynchus nycteribiae* on its abdomen. Cheile Turzii, Romania. Photo by Walter P. Pfliegler

single host species. Traditionally, these associations have been categorized as monoxenous (one host species), stenoxenous (a few closely related host species) or polyxenous (many host species) (Wenzel et al. 1966). Historically, bat flies were largely viewed as not particularly host specific, owing to the fact that bat species often share roosting environments, and that records of many bat fly species were known from a variety of host bat species (Dick and Dittmar 2014). However, carefully controlled collection techniques have made it clear that many early records were attributable to human error such as sampling contamination, and a new consensus has emerged that bat flies are remarkably host specific, given their size, mobility, life cycle, and the multi-species roosting associations of their hosts (Dick 2007; Dick and Patterson 2007). Exceptional cases are known, however, where a single bat fly species may parasitize several well-demarcated host species yet show no population structuring, as appears to be the case with the nycteribiid *Cyclopodia horsfieldi* on three species of *Pteropus* bats in Asia (Olival et al. 2013). In other cases, it is quite possible that less-specific bat fly species may represent unrecognized species complexes (cryptic species) mirroring species complexes that are recognized in bats, e.g., in the genus *Sturnira* (Velazco and Patterson 2013, 2014). We note that such host-specific, near-cryptic segregation has also been detected in Laboulbeniales fungal ectoparasites of certain insects (Haelewaters et al. 2018a). The degree of specificity and the dynamics driving it is important, as it informs the potential for flies to encounter novel hosts in the environment (e.g., in roosts), to potentially spread hyperparasites such as Laboulbeniales to novel host species, or to move pathogens from host to host, including potentially to humans.

21.3 Ectoparasitic Fungi on Arthropods

There is little scientific consensus in the field of mycology, but for the acknowledgement that it will take many, many years to describe the vast diversity that lies in the Kingdom Fungi. Currently, 135,000 species are accepted (Hibbett et al. 2016), but estimates range from 1.5 to six million species of fungi. The number of fungal parasites is particularly underestimated. Focusing on insect-specific fungi, only 1.5% is estimated to be currently known (Mueller and Schmit 2007). These include necrotrophic and biotrophic parasites (Benjamin et al. 2004). Whereas necrotrophs kill their hosts and then use dead host cells as a source for nutrition, biotrophic parasites require a living host. A third type, "hemibiotrophy," involves an initial biotrophic phase followed by a switch to necrosis (De Silva et al. 2016). An example is *Magnaporthe grisea*, the causal agent of blast diseases in agriculturally important crops.

One group of fungal biotrophic parasites are the Laboulbeniales (Ascomycota, Laboulbeniomycetes). They live as external parasites on arthropod hosts. Laboulbeniales fungi are microscopic in size, have peculiar morphology and complicated taxonomy, and are vastly understudied—even neglected—by the mycological community. The name *Laboulbeniales* honors the French entomologist Joseph A. Laboulbène, who was one of the first to observe these fungi back in the 1840s. Another French entomologist, Auguste Rouget, independently from Laboulbène, made observations of what he thought were antennal segments of a *Brachinus* ground beetle. Only later did he recognize them as living organisms (Rouget 1850). The earliest account of Laboulbeniales in the literature dates from 1849. An anonymous summary of a meeting of the *Wissenschaftsfreunde* mentioned that Ferdinand J. Schmidt had found clusters of bristles on *Nebria* "*stentzii*," which he had identified as parasitic plants. Mayr (1853) thought the hairlike structures on *Nebria* beetles were outgrowths of the insect integument, but he described differences in the structures on younger and older host specimens. It was Robin (1852, 1853) who recognized these organisms as fungi. A few years later, two species of bat fly-associated Laboulbeniales were described as acanthocephalan worms (Kolenati 1857).

Laboulbeniales, colloquially dubbed *beetle hangers* by Mordecai C. Cooke in his book *Vegetable wasps and plant worms: a popular history of entomogenous fungi, or fungi parasitic upon insects*, are one of three orders in the class Laboulbeniomycetes, the others being Herpomycetales and Pyxidiophorales (Haelewaters et al. 2019). All three orders comprise fungi that are obligately associated with arthropods either as biotrophs (Herpomycetales, Laboulbeniales) or for dispersal (Pyxidiophorales). What sets the Laboulbeniales apart is their diversity, with 2325 known species and many more awaiting discovery and description. On the other hand, the orders Herpomycetales and Pyxidiophorales together include fewer than 50 accepted species. Laboulbeniales require a single host for successful development. A two-celled ascospore adheres to the new host and either penetrates the cuticle making contact with the body cavity for nutrition and support or remains superficially attached without penetration (Tragust et al. 2016). Subsequent divisions of the ascospore lead to a three-dimensional, multicellular unit of determinate growth, or a *thallus*. This sets the group apart from other fungi, which usually form hyphae and are recognized by unlimited growth.

The host range of Laboulbeniales as a group includes three subphyla of arthropods: Chelicerata, Myriapoda, and (mainly) Hexapoda. About 80% of described species have a beetle host (Coleoptera); other hosts are mites (Acari), harvestmen (Opiliones) (Chelicerata), millipedes (Diplopoda) (Myriapoda), cockroaches and termites (Blattodea), earwigs (Dermaptera), flies (Diptera), true bugs (Hemiptera), ants (Hymenoptera), crickets and allies (Orthoptera), lice (Psocodea), and thrips (Thysanoptera) (Hexapoda). Despite this wide host distribution, most Laboulbeniales show strict host specificity (De Kesel 1996; Haelewaters et al. 2018a). Others are "habitat specific"; they have multiple hosts in phylogenetically unrelated groups that occur in the same micro-habitat, such as ant nests and subterranean caves (De Kesel and Haelewaters 2014). There are two other types of specificity; some taxa are restricted to a specific position of the host integument (= position specificity) or to a given host sex (= sex-of-host specificity). An extreme example is *Chitonomyces unciger*, which only occurs on the claw of the left posterior leg of male *Laccophilus maculosus* beetles. There are opposing views as to the taxonomic significance of morphological variability in thalli among host species, between sexes of the hosts, and among locations on a given host. Different morphologies relating to the different types of specificity are treated as distinct species by some researchers, or as morphotypes (*formae*) of the same biological species by others. However, DNA-based studies at the species level have shown that morphology *alone* may be a poor means to understand the diversity of Laboulbeniales.

The small community of researchers studying Laboulbeniales primarily focuses on taxonomy (description of species). In recent years, however, several papers have resolved species-level taxonomic problems and clarified phylogenetic relationships among the order. Studies of the Laboulbeniales have long been challenging for multiple reasons. Thalli are microscopic in size, which requires micro-manipulation techniques and specific tools. Thalli are also long-lasting and so must absorb impacts and friction during their entire existence on a given host. This requires tough and resilient cells, which are difficult to break open. Hosts can carry different species of Laboulbeniales, but they can also carry multiple morphological forms (*morphotypes*) of the same species as well as multiple morphotypes of different species. Given this, DNA extractions ideally should be performed of single thalli. Many species are heavily pigmented with melanin in their cell walls, which interferes with molecular protocols to amplify regions of interest. Finally, contrary to the majority of fungi, researchers have not been able to grow Laboulbeniales in culture.

The relationships of the order Laboulbeniales to other members of the class Laboulbeniomycetes are far from established, with several lineages underrepresented in terms of taxa and sequence data. In addition, its intra-ordinal relationships are completely unresolved. Two major ordinal classifications have been proposed, one by Roland Thaxter in 1896, which he updated in 1908, and the other by Isabelle I. Tavares in 1985. Both are entirely based on morphology. The only criterion for grouping taxa in Thaxter's system (1896) was the formation of spermatia. He separated the then "family Laboulbeniaceae" in two "groups," the Exogenae and Endogenae. The Exogenae included genera with species that produce spermatia (gametes) on the appendages. The Endogenae, on the other hand, comprised taxa in which spermatia are formed inside of specialized organs, antheridia. This group included two "orders" depending on the way spermatia are discharged. In many genera, multiple simple antheridia are formed; these are individual cells, usually with a slender neck functioning as a discharge tube. In other genera, compound antheridia are produced: antheridial cells are arranged such that spermatia are released into a chamber with one common exit.

In *Monoicomyces*, the compound antheridia are distally rounded with an indistinguishable pore, whereas the compound antheridia of *Peyritschiella* have an elongated neck. Recent preliminary phylogenetic reconstructions of the Laboulbeniales (e.g., Goldmann and Weir 2018) show that compound antheridia originated more than once. Joseph H. Faull had pointed this out in 1911, but it took until Tavares for a new classification scheme to be introduced. Tavares (1985) used perithecial development and wall structure as well as antheridial characters in her classification. She divided the order into two suborders, three families, six subfamilies, as well as many tribes and subtribes. Some features that were considered by Tavares are phylogenetically informative, such as the number of perithecial wall cells, which seems to be undergoing a progressive reduction through evolutionary time. However, quite a number of higher taxa introduced by Tavares are polyphyletic, meaning that the taxa are placed in these unnatural groups that have derived from different common ancestors. For example, the Stigmatomycetinae tribe consists of 40 genera, but recent studies do not include half of these genera and they belong to multiple, unrelated clades (Goldmann and Weir 2018, Haelewaters et al. 2018c). In conclusion, the phylogeny of the Laboulbeniales order is in complete disarray. More taxa need to be sampled and more sequence data are needed in order to resolve this.

21.4 Bats, Bat Flies, and Laboulbeniales Fungi

Jonathan Swift, when writing his 1733 poem about multitrophic interactions—*The vermin only teaze and pinch/Their foes superior by an inch/So, naturalists observe, a flea/Has smaller fleas that on him prey;/And these have smaller still to bite 'em,/And so proceed ad infinitum*—might not have realized that organisms involved in such interactions probably outnumber free-living organisms. Although understudied, we know of a number of hyperparasites specific to bats. This knowledge has resulted from comprehensive studies, sometimes triggered by accident during fieldwork. The bats–bat flies–Laboulbeniales project that is the focus of this chapter began with a single bat fly collected as *bycatch* by colleague and collaborator Jasmin J. Camacho. She had collected it along with other materials and preserved it in ethanol because she had remembered that her friend "did something with insects and fungi." It would take a couple of months until that friend (DH) showed some interest in that bat fly. The first attempt to identify the fungus was a failure and it has been a steep learning curve since that time. But now, just 4–5 years later, that small project has led us to investigate 12000 bat flies in total with other collaborators in the United States, Panama, Germany, Hungary, and Switzerland.

The addition of a second level of parasitism to the study of bats is relatively new. Bats serve as host for all kinds of ectoparasites, including flies (Diptera), true bugs (Hemiptera), fleas (Siphonaptera), ticks and mites (Acari), and earwigs (Dermaptera). Some of those can be parasitized by other pathogens or parasites. For example, bat flies appear to be vectors for *Bartonella* bacteria, which are causal agents for zoonotic diseases in mammals (including humans) (Morse et al. 2012b). Also several lineages of bacterial endosymbionts are associated with bat flies. These associations are ancient in evolutionary time but due to a lack of integrative studies, we know little about the nature of these relationships (Morse et al. 2012a). When parasites (bat flies) serve as hosts to other parasites (Laboulbeniales fungi), we can see the bat itself as a *microhabitat*. A microhabitat can be defined as a small, localized environment within a larger ecosystem. For example, standing tree remnants and fallen logs are important microhabitats that serve as nutrient and energy resources and provide protection for invertebrates, amphibians, small mammals, plants, and fungi. In the bat microhabitat, options exist for host shifts of Laboulbeniales between bat flies. This is where things become interesting from an evolutionary point of view. Divergent natural selection among populations of Laboulbeniales fungi that are now exploiting different bat flies may ultimately lead to reproductive isolation and the formation of new species (Mayr 1942; Dobzhansky 1951; Schluter 2000).

21.4.1 Laboulbeniales on Bat Flies

Around 10% of Laboulbeniales species parasitize flies. Laboulbeniales that are associated with flies belong to eight genera: *Arthrorhynchus*, *Dimeromyces*, *Gloeandromyces*, *Ilytheomyces*, *Laboulbenia*, *Nycteromyces*, *Rhizomyces*, and *Stigmatomyces*. The eponymous genus *Laboulbenia* is by far the largest genus with hundreds of species, of which only 24 species are described from flies. The second-largest genus in the order is *Stigmatomyces*, with 171 described species that are all described from flies, although none from bat flies. Thus far, four genera have been reported from bat flies: *Arthrorhynchus*, *Dimeromyces*, *Gloeandromyces*, and *Nycteromyces*. *Arthrorhynchus*, *Gloeandromyces*, and *Nycteromyces* are specific to bat flies, whereas *Dimeromyces* has a wide host distribution.

21.4.1.1 *Arthrorhynchus*

Arthrorhynchus (Figs. 21.2 and 21.3a) is restricted to Eastern Hemisphere bat flies of Nycteribiidae. Four species are currently known, but this number is expected to increase in coming years. As an interesting *fait divers*, the first two species in the genus were described in the nineteenth century as acanthocephalan worms (Kolenati 1857). Peyritsch (1871) described a species *Laboulbenia nycteribiae* and considered both of Kolenati's species as synonyms of the new taxon. Later, realizing his species was not actually a representative of the genus *Laboulbenia*, he established a new genus to accommodate this species: *Helminthophana nycteribiae* (Peyritsch 1873). Thaxter (1896) followed Peyritsch's opinion but later retained the genus *Arthrorhynchus* and described two additional species so that there were three species in the genus: *Arthrorhynchus cyclopodiae*, *A. eucampsipodae*, and *A. nycteribiae* (Thaxter 1901). A fourth species, *A. acrandros*, was described by Aldo Merola (1952).

It is fair to say that the taxonomic history of the genus has been complicated. In addition, the current taxonomic status of these four species is unclear because of the lack of sequence data. Since their description, no-one has ever really done any work in this genus, except for Meredith Blackwell. At the 1979 Annual Meeting of the Mycological Society of America (Stillwater, OK), she reported on host associations, intraspecific morphological plasticity, and the description of developmental stages of thalli. Blackwell had screened 2517 nycteribiid bat flies for presence of Laboulbeniales fungi and observed thalli on 56 bat flies (= parasite prevalence of 2.2%). These results were later published in the journal *Mycologia* (Blackwell 1980a, b). It took almost four decades until this genus was dusted off again, with the publication of a paper in *Parasites and Vectors*. In this paper, Haelewaters et al.

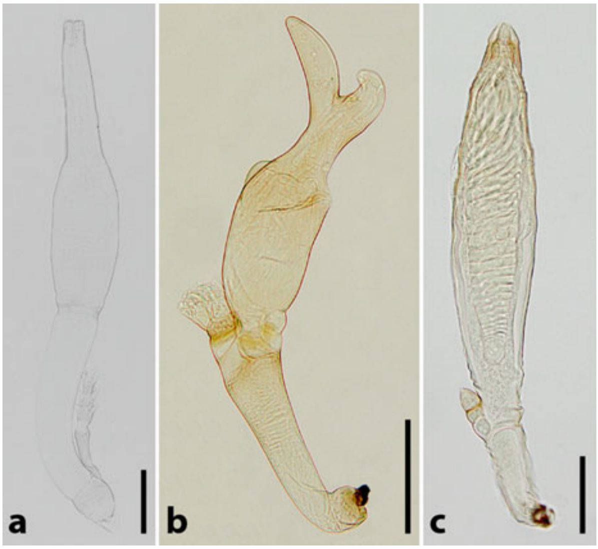

Fig. 21.3 Thalli of bat fly-associated Laboulbeniales: (**a**) *Arthrorhynchus nycteribiae* (D. Haelew. 1015c, Felsőtárkány, Hungary); (**b**) *Gloeandromyces streblae* forma *sigmomorphus* (D. Haelew. 1099b, Gamboa, Panama); and (**c**) *Nycteromyces streblidinus*, a female thallus (D. Haelew. 1012a, Michoacan, Mexico). Scale bars: **a** = 100 μm and **b**–**c** = 50 μm

(2017a) examined 1494 bat flies and found 45 infected ones (= prevalence of 3.0%). The authors built a host-parasite-parasite network, discussed distributional and host ranges, and reported that *Arthrorhynchus* spp. may have a preference for female over male bat flies.

Celebrating the 40th birthday of the first-ever talk on *Arthrorhynchus*, Tamara Szentiványi and colleagues (2019) presented a poster at the International Bat Research Conference in Phuket, Thailand about the current conceptions of host specificity, species-level diversity, and geographic distribution. Preliminary molecular data show that *Arthrorhynchus eucampsipodae* and probably also *A. nycteribiae* are complexes of multiple species, which are segregated by host fly species. It is too early to make taxonomic decisions, but this is not a stand-alone case in the Laboulbeniales. *Hesperomyces virescens* is a taxon associated with over 30 species of ladybirds (Coleoptera, Coccinellidae). Using an integrative approach—combining morphometric, molecular phylogenetic, and ecological data—we found that *H. virescens* consists of different species, each adapted to an individual ladybird host (Haelewaters et al. 2018a). Discovering the same pattern of speciation in another genus of Laboulbeniales gives us insight to the untold diversity in this order. Current estimates predict up to 75,000 species in the order (Weir and Hammond 1997) but even this number does not incorporate the idea of species complexes.

21.4.1.2 *Dimeromyces*

Dimeromyces is one of the largest genera in the order, with about 115 described species, of which only two are known from bat flies (Rossi et al. 2016). The genus is dioecious, which means that (male) antheridia and (female) perithecia are housed on separate individuals. Species of *Dimeromyces* parasitize mites (Acari), termites (Blattodea), beetles of many families (Coleoptera), earwigs (Dermaptera), flies (Diptera), ants (Hymenoptera), crickets (Orthoptera), and thrips (Thysonaptera). Only recently, two species of *Dimeromyces* were described from bat flies (Dogonniuck et al. 2019). These are *Dimeromyces capensis* on *Brachytarsina africana* [as *Nycteriboscа*] from South Africa, and *D. streblidarum* on *Brachytarsina amboinensis* [as *Nycteribosca*] from the Philippines. The two new species form a blackened foot, which is the (single) point of attachment to the host. The presence of a simple foot, however, is not a generic character, and this was already observed by Thaxter (1908).

Several species of *Dimeromyces* from earwigs and flies carry a haustorium. A haustorium is a simple or branched rhizoidal apparatus that penetrates the host's integument to provide added stability and to increase surface area for nutrient uptake. Haustoria make contact with the body cavity (haemocoel) and draw nutrients from it. There had been a long-running debate whether all species of Laboulbeniales produce haustoria—simple and minute or well-developed—until Tragust et al. (2016), using light and electron microscopy, found no evidence for any penetration in four species of Laboulbeniales. Some hypothesize that the presence of a haustorium may trigger certain defense mechanisms of the host, which, in turn, requires physiological adjustments of the fungus (Haelewaters and De Kesel 2017, 2020). All this may facilitate specialization and reproductive isolation (speciation). Currently insufficient data are available to test this hypothesis across the order. As is the case for *Dimeromyces*, several other genera include species with a simple foot as well as species with a haustorium, including *Gloeandromyces* and *Nycteromyces*.

21.4.1.3 *Gloeandromyces*

Gloeandromyces was described by Thaxter (1931) to accommodate two species he had earlier reported as *Stigmatomyces* (Thaxter 1917). The fan-like organization of the appendage in *Gloeandromyces* is different from *Stigmatomyces*, and the gelatinous disorganization of the appendage structure in mature thalli is often indecipherable. After description, both species had not been found until a century later, when Haelewaters et al. (2017b) re-discovered them in Central America. A third species was described in the same paper, from *Trichobius dugesioides* bat flies in Gamboa: *Gloeandromyces pageanus*, named after long-time Panamanian collaborator Rachel A. Page. Most recently, a fourth species was described, *Gloeandromyces dickii*, from *Trichobius joblingi* in Nicaragua and Panama. The fungus was originally found on bat flies that were part of a loan of 7792 specimens kindly provided by CWD, and so was named in his honor.

Based on sequence data for the large subunit ribosomal DNA, Haelewaters and Pfister (2019) pointed out that *G. pageanus* is a conglomerate of three morphotypes or *formae* in two clades. The first clade, with *G. pageanus* f. *pageanus*, only occurs on *T. dugesioides*. This morphotype always seems to occur on the dorsal part of the thorax. The second clade is most-often observed on *T. jobilingi* and consists of two morphotypes, one of which is specific to the base of the wings (*G. pageanus* f. *alarum*) and the other does not show any positional preference the host (*G. pageanus* f. *polymorphus*). In other words, in *G. pageanus*, two mechanisms seem to drive diversity: host specialization and phenotypic plasticity leading to position-induced morphological alterations. Also in *G. streblae*, the same two mechanisms are observed; *G. streblae* forms two clades segregated by host, and one morphotype is recognized at the last segment of the abdomen (*G. streblae* f. *sigmomorphus*, Fig. 21.4b). In both *G. pageanus* and *G. streblae*, even though there is divergence of hosts, no speciation has occurred. This may be a case of either *incipient* or *ephemeral* speciation (Rosenblum et al. 2012).

21.4.1.4 *Nycteromyces*

Nycteromyces is a small genus with only two described species, both occurring on Streblidae. *Nycteromyces streblidinus* (Fig. 21.4c) was described by Thaxter (1917) on a *Strebla wiedemanni* (Streblinae), but since then it has only been found on species of *Metelasmus* (Streblinae), *Aspidoptera*, *Eldunnia*, *Megistopoda*, *Speiseria*,

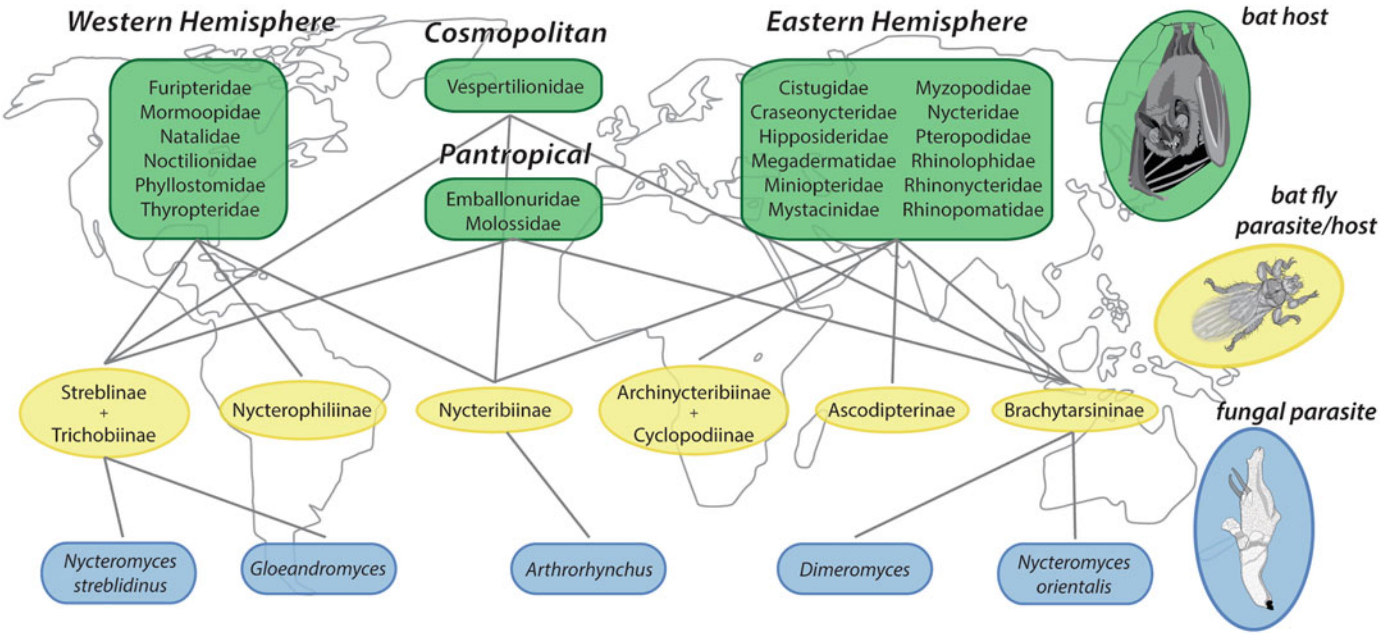

Fig. 21.4 An overview of the multitrophic associations between families of bats, subfamilies of bat flies, and genera/species of Laboulbeniales fungi, presenting the geographic distributions of the taxonomic groups as currently understood. Illustrations by Damond Kyllo. Updated and modified from Haelewaters et al. (2018b)

and *Trichobius* (Trichobiinae) (Haelewaters et al. 2018b; Dogonniuck et al. 2019, unpublished data). The second species, *Nycteromyces orientalis*, was described recently from *Brachytarsina* spp. [as *Nycteribosca*] (Brachytarsininae) (Dogonniuck et al. 2019). Whereas *N. streblidinus* is limited to New World streblids, *N. orientalis* is associated with an Old World streblid genus. From a biogeographical point of view, this poses an intriguing question: Does *Nycteromyces* have a Gondwanan origin? Southern Hemisphere biota have been shaped by the fragmentation of the supercontinent Gondwana, which caused the isolation and diversification of ancestral Gondwanan taxa on each respective landmass. *Nycteromyces orientalis* is very different from *N. streblidinus*, with a series of cells that give rise to multiple perithecia (Dogonniuck et al. 2019), whereas in *N. streblidinus* only a single perithecium is produced (Fig. 21.4c). However, this would be less surprising given a potential Gondwanan origin. Similarly, in another group of fungi (genus *Amanita*), researchers have identified taxa in southern South America to be grouped with relatives from Australia in a clade dating back to 34.5 million years ago, which fits with the timing of the fragmentation of South American, Australian, and Antarctic Plates (Truong et al. 2017).

21.4.2 Parasite Prevalences

Based on the study of 2517 nycteribiid bat flies, which were screened for the presence of Laboulbeniales fungi, a parasite prevalence of 2.2% was found (Blackwell 1980b). More recently, Haelewaters et al. (2017a) screened 1494 nycteribiid bat flies, and found 45 specimens to be infected with either *Arthrorhynchus eucampsipodae* or *A. nycteribiae* (3%). During a seven-night expedition in a Panamanian cloud forest (Walker et al. 2018), 227 bats were captured, resulting in 437 bat flies (436 streblids + 1 nycteribiid) of which 30 streblids carried thalli of Laboulbeniales (7%). Szentiványi et al. (2018) captured 270 *Miniopterus schreibersii* bats across Europe, resulting in 667 nycteribiid bat flies of which 60 were infected (9%). And finally, a comprehensive study of 7949 bat flies from both the New World and Old World resulted in a prevalence of only 4.6% (Haelewaters et al. 2018c).

These low percentages have been explained by life history. Ascospore transmission between bat flies likely occurs only on the bat through direct contact (De Kesel 1995). Based on the Smithsonian Venezuelan Survey collections, of 79 bat species that were captured five or more times and infested with bat flies, 7395 individual bats yielded 36,631 flies with an overall mean intensity of 4.95 streblid flies per bat host (Patterson et al. 2007). From 1594 bats of 28 species captured in central Europe, Haelewaters et al. (2017a) collected 1494 nycteribiid bat flies, with an average number of 1.79 flies per individual bat host. The mean intensity of bat fly parasitism is highly variable and dependent on myriad factors including bat host sex, species, roost type, and parasite life history, but in general it seems that the number of times a Laboulbeniales-infected bat fly comes into contact with another bat fly of the same species (or of a species that serves as a host to that Laboulbeniales species) is very low.

21.4.3 Effect of Climate

The presence and parasite “load” of Laboulbeniales infections can be influenced by biotic factors such as host age, sex, and aggregation behavior (Nalepa and Weir 2007; Báthori et al. 2018). But how abiotic factors affect the temporal and spatial distribution of these fungi is unexplored, except for one recent study by Szentiványi et al. (2019). These authors found a higher likelihood of presence of *Arthrorhynchus* on bat flies in habitats with low annual mean temperature and humidity. One of the factors that may play a role is the temperature-dependency of the immune response of arthropods; higher temperatures contribute to disease resistance in insects. In general, our knowledge on how climatic elements might alter host behavior or ectoparasite transmission, presence, and prevalence is still very limited.

21.4.4 Cospeciation Patterns

Coevolutionary studies can shed light on specific instances of host shifting and cospeciation. The application of molecular phylogenetic methods with various symbiotic associations has revealed patterns of congruence between the individual partners. These patterns can resolve questions regarding whether symbionts have diversified in parallel (cospeciation or coevolution) or reveal instances of host shifting over their evolutionary lineages. Such studies can also be applied to multitrophic systems. For example, the symbiosis between fungus-growing ants, the fungi they cultivate for nutrition, and the microfungal parasites of the ants’ fungus gardens has a coevolutionary history dating back tens of millions of years. At the deepest nodes, the phylogenies of these three partners are in perfect congruence, which implies the symbiosis results from a tripartite coevolution (Currie et al. 2003).

A preliminary coevolutionary study of Laboulbeniales fungi and their bat fly hosts resulted in congruence of the basal-most Old World clades (Haelewaters et al. 2018c). Bat roosting behavior may explain some of the other patterns that were observed. However, a major issue in the accurate interpretation of coevolutionary patterns is that the taxonomy of bat fly-associated Laboulbeniales fungi has not yet been resolved. For example, *Nycteromyces streblidinus* has bat fly hosts in seven genera. If this species turns out to be a complex of multiple species segregated by host, then the fungus phylogeny will look very different (multiple nodes) compared to our current understanding of *N. streblidinus* as a single species (a single node). In the case of multiple *Nycteromyces* species within *N. streblidinus* (sensu lato), different conclusions will need to be drawn from a coevolutionary study. The same is the case for *Arthrorhynchus* spp., which we now consider to be species complexes (Szentiványi et al. 2019).

21.5 Synergistic Interactions Leading to Uncharted Collaborations

It has been hypothesized that the majority of known species on earth exhibit characteristics of parasitism broadly defined. Conversely, parasite species necessarily associate with host species. Hence, it is not an overstatement that nearly all living beings are part of one or more host-parasite associations. Much of our understanding of the diversity, ecology, and evolution of parasitism was built upon a foundation of natural history collections, assembled by field biologists practicing traditional, often taxon-specific studies such as mammalogy, ornithology, entomology, and mycology. For example, parasites of mammals are routinely collected by mammalogists while conversely, mammals are collected by parasitologists in order to obtain their parasites. The synergy between mammalogists and parasitologists is rich and longstanding, if not assumed. For simplicity, we refer to a *parasitologist* as anyone studying parasitic organisms, whether fungi, bacteria, protozoan, or metazoan. Synergism between mammalogists and parasitologists may be nearly as old as those fields of inquiry. Correspondence between Charles R. Darwin and Henry Denny dating back to January 1865 focused on lice and various aspects of their host associations, specificity, as well as speciation and species boundaries (Darwin 1865).

21.5.1 Early Expeditions

With respect to bats and bat flies of the Western Hemisphere, specimens collected during early zoological expeditions were examined by numerous taxonomic specialists of mammals and parasites alike. The book *Ectoparasites of Panama* (Wenzel and Tipton 1966a) was a seminal and systemic work on various ectoparasitic groups collected from Panamanian mammals. This effort resulted from close collaborations between federal agencies in Panama (Gorgas Memorial Laboratory) and the United States (NIH Middle America Research Unit, the US Army, and the Smithsonian Institution). During the course of this highly collaborative study, more than 360 species of ectoparasites in over 120 genera were collected, of which 15 genera and 115 species were new to science. Moreover, the bats captured and surveyed for ectoparasites yielded around 12,000 specimens of streblid bat flies, with 44 species described as new. The mammalogical aspects of the survey were overseen by Charles O. Handley, Jr. of the Smithsonian Institution.

Another massive and collaborative effort was undertaken about a decade later in Venezuela, from 1965 to 1968, with the focus on mammal–parasite–habitat relationships. This was the Smithsonian Venezuelan Project, again with the mammalogical aspects overseen by Handley. This survey sampled bat flies and other ectoparasites from more than 6800 bats of 95 species, yielding over 36,000 specimens of streblids of 115 species and 22 genera. Two genera and 45 species were new to science (Wenzel 1976). These two massive collections alone produced nearly 50,000 specimens of streblid bat flies representing at least 40% of known collections for this group.

21.5.2 Recent Expeditions

Our current work in Panama, which has been a collaborative effort between researchers from Harvard University (USA), the Smithsonian Tropical Research Institute (Panama), the Universidad Autónoma de Chiriquí (Panama), and the University of Ulm (Germany), focuses particularly on the tripartite interactions. A three-month field trip capturing bats in Gamboa and at Soberanía National Park in the Canal Zone, in Chilibre, and at Chucantí Nature Reserve, resulted in 634 bats, of which 367 carried bat flies. Overall, our fieldwork in 2015–2020 has thus far resulted in the study of 4279 bat flies, of which 228 carried Laboulbeniales fungi (5.3%). Two new species and four morphotypes of *Gloeandromyces* have been described, and at least two more species await description. A one-month field trip in Cusuco National Park, Honduras in 2019 led by Operation Wallacea yielded 601 bats, of which 258 carried ectoparasites (bat flies, mites, and ticks). The study of these ectoparasites is still in progress.

21.5.3 Scientific Attention for Bats and Bat Flies Through Time

All of this fieldwork and related systematic activities have fueled the publication of catalogues and keys to regional bat fly faunas (Wenzel et al. 1966; Theodor 1967; Wenzel 1976; Guerrero 1993; Graciolli and de Carvalho 2001; Dick and Miller 2010). Keys, descriptions, diagnoses, and an increasing number of reference specimens have greatly simplified problems of identification, stimulating both systematic and ecological studies on the bat flies and additional investigations of their parasitic relationships. Moreover, the monumental and pioneering work of Wenzel et al. (1966), Theodor (1967), and Wenzel (1976) paved the way for population-level studies of bat flies and their host bats by researchers and their students alike.

For example, at an early NASBR meeting (then called the Second Southwestern Symposium on Bat Research) in November 1971, William L. Overal gave an oral

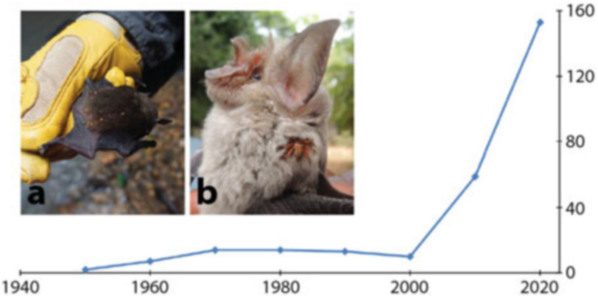

Fig. 21.5 Total numbers of publications per decade citing Streblidae and/or Nycteribiidae. Inset: Bats and their ectoparasites. (**a**) Several streblid bat flies crawling through the fur of a *Pteronotus mesoamericanus*, Parque Nacional Soberanía, Panama. (**b**) A *Rhinolophus* bat with a large nycteribiid bat fly (*Penicillidia fulvida*), coastal Kenya

presentation entitled "Host relationships of the batfly, *Megistopoda aranae*, a parasite of *Artibeus jamaicensis* in Panama." Later, Overal received his Ph.D. degree based on the study of North American *Trichobius* bat flies (Overal 1980a). His dissertation committee consisted of George Byers (Chair), Charles Michener, and Robert Beer. Overal acknowledged having received invaluable assistance by Rupert Wenzel as well as other well-known bat biologists such as Merlin Tuttle and Thomas Kunz. Overal (1980b) subsequently published his study on the life cycle of *Megistopoda*.

Illustrating the growing trajectory of work on bat flies, a Web of Science search on 22 Aug 2019 produced 272 unique references (one article was not dated) published between 1901 and 2019 that used the terms "Streblidae" (196 hits), "Nycteribiidae" (175 hits), or both terms (99 hits). The resulting graph (Fig. 21.5) shows a recent exponential increase in scientific attention to a crucial link in this tripartite system, and bodes well for future understanding of both host-parasite interactions in which it is involved. This remarkable increase in attention is also obvious from talks and posters presented at scientific meetings—NASBR and other—between 1971 and 2019 (Supplementary File 21.1).

21.6 Future Research Directions

In a remarkable chapter entitled *Some relationships between mammal hosts and their ectoparasites*, Wenzel and Tipton (1966b) described many patterns of parasite-host associations and posed numerous outstanding questions that have motivated decades of inquiry into the ecology and evolution of parasite host associations. The phenomena highlighted and discussed in that chapter included host specificity, coexistence and competitive displacement, as well as altitudinal zonation and zoogeographic relationships between parasites and hosts. Many of the broad questions posted in this seminal chapter are still being addressed five decades later. Similarly, many of these same broad questions are also posed in the tripartite system of bats, bat flies, and Laboulbeniales fungi.

One of the most important questions that we aim to address concerns the effect of habitat on parasitism of bat flies by ectoparasitic fungi (Haelewaters et al. 2018b, Haelewaters and Martin 2019). We hypothesize that habitat disturbance causes parasite prevalence to increase, in line with the *dilution effect* (Fahrig 2003). The main idea is that healthy ecosystems reduce the average risk of disease, and habitat loss results in an elevated risk of wildlife diseases through a decline in overall biodiversity. However, parasitic reactions to habitat alterations depend on the parasite and its associated host. Given the low parasite prevalence encountered for Laboulbeniales on bat flies, we stress the need for large, non-biased datasets resulting from focused multitrophic fieldwork. We call for global collaborations with bat scientists and organizations. The aim is to keep building on our dataset of currently 11936 bat flies with associated metadata from the Western and Eastern Hemispheres to (1) define ecological and life history traits that are correlated with parasitism of bats by bat flies and of bat flies by Laboulbeniales fungi, and (2) fully understand (co)evolutionary relationships through the generation of phylogenetic and phylogenomic-scale data.

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Afterword

Dina K. N. Dechmann

As I write this in my home office, the COVID-19 pandemic has the world firmly in its grip, with many conferences cancelled, and so the 50th North American Society for Bat Research (NASBR) meeting, to be held in Tempe, Arizona, has been postponed a year too. This is the first meeting in 50 years that will not take place as planned. Although I can celebrate only 22 years of NASBR myself, I have seen the world of bat-related research change into an impactful research area and grow almost exponentially from a close-knit family in which everyone knew everybody else and their scientific mothers, fathers and grandparents, into a large global community. NASBR during this time has changed surprisingly little.

I made my way to my first meeting thanks to Swedish researcher Jens Rydell. I was doing my master's field work in Costa Rica at the time, and in spring 1998, Brock Fenton and his lab visited the field site, with several guests, one of whom was Jens. He told me: "Present your work at NASBR, not at a European bat conference; the scientific standards are much higher." And so, I did. My first meeting was 1998 in Hot Springs, Arkansas, and it was incredible for me—the naive, inexperienced Swiss student—to meet the vibrant, inclusive NASBR community for the first time. It was a meeting at which feedback was supportive and encouraging and promoting students was clearly a primary goal. That is when I started to build a scientific network with colleagues, many of whom I consider friends, that has continued to branch and grow in the following two decades. There are few scientific disciplines for which the level of "elbowing" is so low and the atmosphere so collaborative.

It has been a pleasure to see the meeting grow in terms of the number of presentations and participants. Even though the society maintains a first-come first-served policy in terms of accepting presentations, the progress that the community has made in how they approach questions, methods, and analyses is reflected especially in the high quality of the student talks. Because of the inclusive approach

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to accepting presentations, the meeting also always reflects where the scientific focus currently lies. NASBR lets me know, “what’s up”? I remember meetings with entire days committed to wind power or white-nose syndrome, many of them full of student presentations. That is another aspect for which the word “inclusive” really fits. All the “big names” make a point of attending the student talks and poster sessions too. NASBR is a warm and comfortable opportunity for the student and newcomer to network. This has not changed at all as the meeting has grown.

Very much linked to inclusiveness and something that has not changed either is the ability of the work-hard party-hard bat researchers to have a good time. And now is when writing this becomes a little sad for me. To write about NASBR, for me, is to write about Tom Kunz. When I came to my first meeting in Hot Springs, I knew barely anyone, but I was welcomed warmly and before I knew, found myself dancing on a stage with Tom Kunz and his students. And thus, I connect NASBR with Tom, not only because of his unique ability to have fun and his boundless energy, but also because he became a mentor and source of inspiration. As author, book editor, co-author, and advisor, Tom was formative for my career, and I will never forget that morning when, many other students and I, watched the sun rise, with beers in our hands, sitting side by side in a hot spring, with this famous professor, who had no attitude and clearly enjoyed the company of colleagues regardless of age or status. That was and is representative of my NASBR experience as a whole, and such an experience was completely new for me, coming from a much more formal academic environment.

The dedication of the North American bat science community to the society and meeting is unparalleled. Even though it is such a topic-focused meeting, everybody always attends. Every single time. No matter how busy, you make time for NASBR and that is why, due to COVID-19 the meeting was postponed and not cancelled. Congratulations and many thanks NASBR for what you do for bats, science, and every single wide-eyed student attending their first meeting. Here’s to the next 50 years.