Jorge Ortega *Editor*

Sociality in Bats

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Chapter 1
Introduction

Jack W. Bradbury

Abstract Compared with other taxa such as primates or songbirds, studies of bat social behavior and communication are a relatively recent development. Despite this late start, bats now constitute some of the key tests of general theories in behavioral ecology. Here, I briefly review some of the history of research in bat behavioral ecology, and hopefully set the scene for the exciting new extensions presented in this volume.

Fifty years ago, we knew almost nothing about bat social behavior, mating systems, or communication. As this volume clearly demonstrates, what a difference five decades can make! Studies of bat behavior and communication have since added major insights to general theories of social evolution, and broad reviews in *Nature* and *Science* routinely include bat examples. This rapid transformation did not occur in a vacuum, but was due to the confluence of three parallel events: a shift in focus from temperate to tropical bat species, the emergence of the field of behavioral ecology, and the development of new technologies. Since I played some role in the early days of this evolution, Editor Jorge Ortega asked me to provide a bit of historical perspective as an introduction to this volume.

In the 1950s, psychologists studied animal behavior in carefully controlled laboratory experiments, usually with rats or pigeons. Ethologists, by contrast, favored studies of wild animals behaving under natural conditions. Psychologists focused on learning and behavioral flexibility, while ethologists invoked phylogeny and instinct to explain the diversity of behaviors they observed. As that decade progressed, more and more field studies melded behavioral and ecological observations, and enough species in certain taxa such as primates, songbirds, and social insects, were studied to begin making comparisons. It was the latter endeavor that set the scene for the advent of behavioral ecology.

In the early 1960s, a number of universities started research programs in animal behavior. New York's Rockefeller University, where I was then a graduate student,

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hired Donald Griffin in 1965 and Peter Marler in 1966. Although Griffin had discovered bat echolocation over a decade earlier, the topic had only received widespread attention after publication of his 1958 book, *Listening in the Dark*. Marler was a pioneer in the study of song acquisition by birds, and had just published a widely used textbook, *Mechanisms of Animal Behavior*. I became Don Griffin's graduate student in 1966 and joined him that summer in Trinidad where we tried to capture as many bat species as possible, bring them back to the field station's flight cage, and record their echolocation calls. Luckily, members of the Trinidad Rabies Control Unit already knew where to find roosts of most of the 58 species of bats on the island. With their help, I traveled widely collecting subjects, and in the process, being introduced to the diversity of social groupings and roosting preferences of neotropical bats.

Back in New York that fall, I began a dissertation on echolocative target discrimination by the large carnivorous bat, *Vampyrum spectrum*. We had obtained two adult mated pairs, one single adult male, and one female offspring to work with. Besides these bats' marked acuity during target discrimination, I was amazed at their intelligence, and fascinated by the intense and complex communicative exchanges both within and between pairs. They reminded me of canids. At the time, I was also participating in a graduate seminar organized by Peter Marler on animal social behavior. I was assigned two recent papers by John H. Crook to review and summarize for the class. In the first paper (1964), Crook outlined his comparative field studies of the mating systems and ecologies of many African weaver bird species, and concluded that, in contrast to the current dogma in ethology, ecology was a better predictor of mating system than phylogeny. In his subsequent 1965 review, he extended his case to all birds. While Crook was not the only person then using species comparisons to look for adaptive patterns, his weaver bird study was surely the most persuasive, and helped stimulate refinements that became the "comparative method" of evolutionary biology (Harvey and Pagel 1991).

I became fascinated by the notion that tropical bats might be a suitable system in which to test Crook's hypothesis. My dissertation work was going well and neither Don Griffin nor I thought a late switch in topics was wise. But I began laying the groundwork for a postdoctoral project in Trinidad to mount such an effort. I read every published account of bat social behavior I could find, but the vast majority focused on the physiology of temperate bats, with only vague descriptions of their spring maternity colonies and fall swarming. A few tantalizing hints about tropical species did turn up. For example, an early twentieth century expedition to the Congo Basin by the American Museum of Natural History reported male hammer-headed bats (*Hypsignathus monstrosus*) aggregating at dusk in riparian forest and calling "like frogs" (Allen et al. 1917). Having seen manakin leks in Trinidad and hearing colleague Haven Wiley describe the communal displays of male sage grouse, this sounded like lek mating to me. D.R. Rosevear (1965) noted that males of most of the West African epomophorine bats (including *Hypsignathus*) called at night, but did not discuss dispersions or functions. John Nelson published a pioneering study of the Australian flying foxes *Pteropus poliocephalus*, *P. scapulatus*, and *P. gouldii* in 1965 describing male defense of roosting tree branches used by females during the mating season. Only a few individual bats were identifiable (by wing wounds) making classification of the mating systems difficult. Andre Brosset's (1966) book on bat biology described varying group sizes and sex ratios in a number of tropical species, particularly emballonurids in India, but did not relate them to any extant mating system classification. Still, enough was described by these authors to confirm my impressions from Trinidad: tropical bats were as diverse socially as they were ecologically. In 1967, I met John Crook at the International Ethological Congress and together we worked out a strategy to test his ideas in neotropical bats. Peter Marler agreed to be my sponsor and helped me secure funding. One month after receiving my PhD in May 1968, I was back in Trinidad.

Despite technical challenges, by August 1969, I had worked out the basic social structures of four neotropical species: the emballonurids *Saccopteryx bilineata* and *S. leptura*, and the phyllostomatids *Phyllostomus hastatus* and *P. discolor*. To facilitate "Crookian" comparisons, I had selected pairs of congeners that I suspected from my prior visit had different social organizations. This turned out to be the case. For example, I found that Trinidad *S. bilineata* lived in colonies of 10–40 individuals in the buttress cavities of large silk cotton trees (*Ceiba pentandra*). Adult males divided the tree surface into contiguous defended territories within which females roosted during the day. Colonies were annually permanent, and many marked males defended the same territories throughout my stay. Some females routinely roosted with the same male, whereas others moved around. Males used a striking variety of visual, acoustic, and olfactory displays to recruit and court females, and to defend their territories against male intruders. Territorial males returned shortly before dawn and emitted complex audible songs to attract returning females. In contrast, sympatric *S. leptura* roosted higher on forest tree boles in groups of 2–6 individuals. Groups turned out to be mated adult pairs and either recent young or visiting unmated individuals. Each group had a set of nearby trees among which it moved on successive days. I saw none of the elaborate displays of the congener; at most, *S. leptura* emitted simple calls at dawn or dusk. Where *S. bilineata* appeared to exhibit resource-defense polygyny and elaborate sexually selected signals, *S. leptura* seemed to live in monogamous pairs with little evidence of sexual selection. These were exactly the kinds of differences Crook found in weaverbirds.

The two *Phyllostomus* species also showed interesting contrasts. *P. hastatus* colonies numbered into the hundreds. They favored limestone caves where they divided into clusters of 20–40 individuals, each cluster packed into a separate pothole in the cave ceiling. The clusters consisted of either many adult females and a single adult male, or all adult males. In census after census, the same individual females were found together in the same clusters. Removal of the single male in female clusters, whether in the cave or in a captive colony I set up in the field station's flight cage, resulted in a new male attaching itself to the female group and chasing off other male intruders. The female composition of such manipulated cluster remained unchanged. This system thus appeared to be female-defense polygyny (harems) as had been described in large ungulates and primates. Whereas *P. hastatus* colonies remained in the same locations all year, *P. discolor* colonies, typically numbering 40–80 individuals of both sexes, moved at intervals of several months between different hollow tree roosts. An entire *P. discolor* colony captured and established in a flight cage at the field station divided up into small harems of 5–8 females, each defended by a single male. While it was hard to see details, a wild colony marked and returned to its hollow tree appeared to maintain this same harem structure at least as long as they used that roost. Female composition in the captive colony harems was more variable than in *P. hastatus* harems, and harem males produced a diverse set of vocalizations not heard in *P. hastatus* colonies. Again, here were two closely related species with striking differences in social organization.

Before beginning a new faculty position at Cornell University in fall 1969, I presented the Trinidad results at that year's Ethological Congress. After my talk, Andre Brosset, recently appointed director of a French research station in Gabon, asked whether I had considered studying any African bats. I mentioned my curiosity about the calling aggregations in *Hypsignathus*. Brosset said he had heard the bats calling but had never watched them. He invited me to come to Gabon to work on these bats. In the summer of 1970, I began the first of five field trips to Gabon. Not only did we confirm that the calling aggregations of *Hypsignathus* were classical leks, in fact amazingly similar to those of sage grouse, but a sympatric epomophorine bat, *Epomops franqueti*, turned out to form exploded leks similar to those of blue and ruffed grouse. This provided another fascinating contrast in social organization between closely related bat species.

The next decade and a half saw an explosion of field research on bats. As a faculty member at Cornell and later at the University of California, San Diego, I found it easy to recruit graduate students and postdoctoral fellows interested in bat research. Graduate student Bernice Tannenbaum extended my work on *Saccopteryx bilineata* by observing matings: these are limited to a short period in December when I had been away from Trinidad for job interviews. She also showed that males are philopatric, a pattern more typical of birds than other mammals. Graduate students William Lopez-Forment examined colony structure and foraging behavior in the emballonurid *Balantiopteryx plicata* in Mexico, and Douglas Morrison studied social organization, mating system, and foraging in the phyllostomatid *Artibeus jamaicensis* in Panama. Graduate student Gerald Wilkinson tackled cooperative blood-sharing by wild vampire bats (*Desmodus rotundus*), and postdoctoral fellow Gary McCracken became the first person to use genetic techniques in bats, showing that harem males fathered most of the offspring in *Phyllostomus hastatus* harems, and that the females in those harems were not kin, again an unusual finding for mammalian female groups. Both Wilkinson and McCracken soon obtained faculty jobs and began sponsoring their own graduate students and postdocs working on bats. Trying to expand our comparative approach, Sandra Vehrencamp and I spent a year in Costa Rica comparing the mating systems, colony sizes and dispersions, foraging ecologies, and demographies of five species of emballonurids (Bradbury and Vehrencamp 1976a, b, 1977a, b). In 1977, I also published a chapter in William Wimsatt's *Biology of Bats* book series summarizing what was then known about bat social behavior and communication, and speculating, based on findings in other taxa, about bat species not yet studied (Bradbury 1977). The intent was to entice other workers to tackle the unstudied species.

While our group certainly contributed to the growing interest in bat field studies, other major forces were at work. The Organization for Tropical Studies (OTS), a consortium of New World universities, hosted field courses in Costa Rica that introduced 50–100 graduate students a year to neotropical biology. It was impossible to ignore the role of bats in tropical communities, and they soon figured heavily in most of the courses. Many graduates of this program later became bat researchers. Independently of our efforts and those of OTS, faculty at other institutions began research programs on bats. Early pioneers in bat field studies included Robert Barclay, Frank Bonnacorso, Andre Brosset, Peter Dwyer, Brock Fenton, Ted Fleming, Ray Heithaus, Donna Howell, Tom Kunz, Andrew McWilliam, Lord Medway, Tim O'Shea, Don Thomas, Dennis Turner, Wolfgang Wickler, Charles Williams, and Don Wilson among many others. The initial emphasis on tropical bats was soon followed by application of the same ideas and methods to temperate bats.

Perhaps the biggest impetus for an expansion of bat research during these years was the emergence of behavioral ecology as a discipline. Whereas most behavior studies in the 1950s focused on "how questions" (e.g., mechanisms of behavior), the 1960s saw the initial asking of "why questions" (e.g., adaptive functions of behavior) and the posing of hypothetical answers. Answering such questions has always been the core task of behavioral ecology. The correlations noted by Crook and his successors between mating systems and ambient ecologies were explained by a series of mating system theories, e.g., Verner and Willson (1966), Lack (1968), Orians (1969), and Emlen and Oring (1977). The different dispersions of animals, which set the scene for mating system evolution, were predicted by the ideal free distribution models of Fretwell and Lucas (1969). Answers to the puzzle of why some animals cooperated whereas others did not were provided by Hamilton (1964), Trivers (1971), Maynard Smith and Price (1973), Parker (1974), and Vehrencamp (1983). The theoretical work of Zahavi (1975) and Lande (1981) triggered a complete revision and expansion of ideas about the role of sexual selection in social evolution. Given their social and ecological diversity, bats were soon "swept up" in the rush to test and refine these theories. Although several early syntheses attempted to integrate the many "why?" questions into a single topic (e.g., Wilson 1975), behavioral ecology did not become an integrated discipline until the publication of John Krebs and Nick Davies' textbook, *An Introduction to Behavioral Ecology* (1981), and the subsequent founding of the International Society for Behavioral Ecology in 1985.

Parallel to the emergence of behavioral ecology was a critical series of technological advances. Behavior of individual bats away from the roost at night was usually impossible to monitor despite being critical to the testing of major theories. The development of miniature radio transmitters in the late 1960s made an enormous difference. I first put radios on bats in the summer of 1971. Adult *Hypsignathus monstrosus* captured in canopy nets on the main study lek were then tracked to their foraging sites and day roosts. I could never have obtained information on either aspect of their biology without the radios. Transmitters and receivers subsequently improved in quality and decreased in size, and have since provided many surprises about bats that could have been obtained in no other way.

As noted earlier, Gary McCracken pioneered the use of genetic tools to assess paternity and relatedness in bat colonies. These tools have also improved markedly since and continue to provide key insights into mating strategies and the economics of social interactions. Portable high frequency microphones, detectors, and recorders have opened up the rich auditory components of bat communication, and refined gas chromatographic tools have provided similar insights into their olfactory signals. GPS receivers allow for detailed mapping studies, and implanted passive transponders ("pit tags") allow for automated monitoring of individual traffic into and out of important locations. Night vision and thermal imaging devices now allow us to view bats behaving in the dark. Fast and powerful computers support data analyses using advanced statistical models. None of these options was available during my first years in Trinidad, and I marvel at the toolkits now available to current researchers.

That brings us to the current volume. Much of the prior fieldwork on bats has pursued Crook's original model by describing mating systems and relating these to ambient ecologies. However, behavioral ecology has made it clear that mating systems are only a part of social evolution. One needs to fill in the other aspects as well. For example, communication is the glue that holds most societies together: while the signal repertoires of a few species, such as *Saccopteryx bilineata*, have been studied in exquisite detail, we have barely scratched the surface for most others. Perhaps comparative studies of bats will create a "Crookian" model for communication systems that complements the one for mating systems. Other topics need similar attention. Ecological studies typically focus on predators, and often ignore the role of parasites and diseases. This imbalance needs to be corrected. As noted earlier, the local recruitment of male instead of female offspring in *S. bilineata* colonies is unusual in mammals. Is it also unusual among other emballonurids? Among other bat families? Whatever the answer, why? Finally, while *Phyllostomus hastatus* groups are highly sedentary and compositionally stable, this is not the case for most bats. Instead, groups vary in size and composition over time, in some cases, quite rapidly. Why? And what consequences does this mixing have for mating systems, acquisition of foraging lore, disease transmission, and other aspect of a species' biology? This volume largely moves beyond the mating system preoccupation of the past and examines each of these collateral topics with new data and fresh ideas. Bats continue to amaze us as we turn to each new page in their story. The new opportunities make an old man want to get back in the game!

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Part I
A Functional Analysis of Bat Sociality

Chapter 2
The Social Organization and Behavior of the Brown Long-Eared Bat *Plecotus auritus*

Joanna Furmankiewicz

Abstract The complexity of the social behavior and social organization of bats arises from the philopatry of females, stable group composition, and hence cooperation with colony members, which in turn influences the mating system of particular species. Understanding the relationship between social organization and mating system is crucial for understanding the behavior of animals. I have studied the social organization and social and mating behavior of a temperate zone species of bat, the brown long-eared bat *Plecotus auritus*, for over 13 years in SW Poland using genetic and behavioral methods. The obtained results enable me to complete and explain the pattern of social organization and mating behavior in this species. *P. auritus* lives in small, stable, and isolated maternity colonies (usually up to 40–50 individuals, including adult resident males) and swarms in underground hibernacula during autumn and spring. Members of the colony use low frequency contact calls when they emerge and return to the roosts and during dawn swarming. The peak of this vocal activity falls between July and September and in the morning. Around 28–38 % of colony members emerge or return in pairs, or sometimes in groups of 3–4 individuals emitting social calls. Before leaving the roost, and after arrival, 10–16 % of bat activity involves tandem flights. This behavior may play a role in the maintenance of social bonds between mates in the roost. Some members of the maternity colonies and solitary males frequently travel to the underground hibernacula from day roosts as far away as 31.5 km every autumn and spring to swarm with bats from other colonies. Swarming populations are large and may gather up to several hundred individuals from several colonies. Swarming bats usually stay in swarming sites for several hours before returning to a day roost, vocalizing and intensively flying, sometimes in groups of 2 or more individuals. Colonies and groups of swarming bats show high gene diversities and low inbreeding coefficients, and they are not genetically isolated by distance, which suggests high gene flow between sites and the mating function of autumn and

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spring swarming. Therefore, inbreeding is avoided in these philopatric and spatially isolated colonies by swarming behavior and mating in hibernacula in the autumn and spring. This work indicates that *P. auritus* appears to be unusual among European temperate zone bat species in its maternity colony composition and stability (resident females accompanied by resident males), biphasic swarming season (in autumn and spring), and distinctive vocal activity in swarming sites and maternity colonies. The social structure and behavior of *P. auritus* is complex and suggests the existence of close and stable society-like groups in this species.

2.1 Introduction

Bats are one of the most gregarious mammals (Kerth 2008). They live in assemblages of different sizes, from several individuals up to several million. In some species, groups are merely aggregations of individuals, showing no social bonds and not engaging in cooperation or other social interactions. However, some bat species form society-like groups, where members show affiliative social behavior, such as allogrooming, allonursing, mutual warming, information transfer, and territory defense (Kerth 2008). Such cooperative behavior is observed mainly in maternity colonies in summer roosts, formed by females to rear their young. In some species, males occasionally join these colonies (McCracken and Wilkinson 2000; Entwistle et al. 2000; Senior et al. 2005). The composition of maternity colonies in some species is stable and the females are strictly philopatric, i.e., belonging to the same matriline; however, usually females are unrelated (Kerth 2006; Entwistle et al. 2000; Burland et al. 2001). A stable group structure and philopatry are assumed to facilitate the evolution of cooperation between members of a group, which is an important benefit of sociality (Greenwood 1980; Emlen 1994) and in turn may result in the higher persistence of a group and more complex social behavior (such as allogrooming, face contact, and individual associations) and social structure (Kerth 2006). Female philopatry, greater natal and breeding male dispersal (movement of adults between breeding attempts), and the evolution of matrilineal social organization have also been suggested as a consequence of a polygamous mating system, which prevails in mammals (Greenwood 1980) including bats (McCracken and Wilkinson 2000). Hence, the social organization of philopatric females may influence the behavior of males and mating systems in particular species (Greenwood 1980; Kerth 2006). The mating systems of bats may involve complex behavior and the organization of mating groups (McCracken and Wilkinson 2000). Moreover, males are often faithful to their mating grounds and occupy them for many years. They sometimes also show cooperative behavior when attracting females, as suggested for the territorial males of Nathusius' pipistrelle *Pipistrellus nathusii* (Jahelková and Horáček 2011).

Cooperative behavior and the maintenance of group stability requires that group members recognize each other, are attracted to each other, and keep contact. These processes are facilitated by communication and individual recognition by means of acoustic (Wilkinson and Boughman 1998; Carter et al. 2008, 2009; Yovel et al. 2009; Chaverri et al. 2010, 2012; Voigt-Heucke et al. 2010; Arnold and Wilkinson 2011), olfactory (Altringham and Fenton 2003), and tactile signals (Kerth 2006). Sound prevails in bat communication, due to their nocturnality and highly developed auditory system, adapted to echolocation (Fenton 2003). There are an increasing number of studies concerning the function of vocalizations in maintaining group cohesion or in locating group members in bats (e.g. Fenton 2003; Chaverri and Kunz 2010; Furmankiewicz et al. 2011).

Adequate understanding of the function of animal signaling and social behavior requires extensive knowledge about the social organization and ecology of the species using a combination of different methods. Bats are good subjects for such investigations. Most are social and their intriguing lives are drawing the attention of an increasing number of researchers from different scientific fields. However, of the more than 1300 bat species, only a small proportion of them have been studied to a greater or lesser extent, and only a few species have been studied long term (e.g. Zubaid et al. 2006). These works contribute to a better understanding of the complexity of bat life history. One of the most intensively studied species of bats is the long-eared bat, *Plecotus auritus*. Studies concerning the social and population structure and ecology of this species have been performed on English (Stebbings 1966, 1970; Boyd and Stebbings 1989; Howard 1995; Park et al. 1998), Scottish (Entwistle et al. 1996, 1997, 1998, 2000; Burland et al. 1999, 2001), German (Heise and Schmidt 1988; Fuhrman and Seitz 1992), and Spanish (Benzal 1991) populations. However, those investigations did not comprehensively describe and explain the different behaviors and social organization of this species. The work on *P. auritus* conducted in SW Poland by myself and my co-workers over the past 13 years has been focused on the organization and behavior of populations swarming in underground hibernacula in the autumn and spring and maternity colonies in the summer. Our work has revealed previously unknown behavioral phenomena and cast new light on our understanding of their behavior.

P. auritus is one of the European temperate zone bat species from the family Vespertilionidae. It is small (5–10 g) and has broad and short wings (Norberg and Rayner 1987), and therefore it can hover and maneuver in close space. Wing morphology presumably influences colony size and distances between roosts and foraging grounds (Entwistle et al. 2000) and inhibits long distance seasonal migration. It is a sedentary species with a maximum known movement between summer roosts and underground sites of 88 km (Strelkov 1969; Gaisler et al. 2003). Maternity colonies are small (usually up to 50 individuals) and isolated. They are composed of females and males and inhabit buildings, tree holes, and bat boxes located close to or within foraging grounds (Stebbings 1966; Heise and Schmidt 1988; Boyd and Stebbings 1989; Entwistle et al. 2000; Duma et al. 2004). The mating period and estrus in females starts in autumn, but ovulation and fertilization takes place in spring after hibernation, similar to other temperate zone bat species. *P. auritus* usually hibernates in underground sites from November until March (Swift 1998; Furmankiewicz and Górniak 2002).

2.2 Methods for the Work Performed on *P. auritus* in Poland

This work was conducted in Lower Silesia in southwestern Poland, located at approximately 50° N and 16–17° E. The landscape of this region varies from agricultural and partly deforested lowlands (Silesian Lowlands) and hills (Sudetic Foreland) to the afforested Sudety Mountains (the highest peak is 1602 m a.s.l.). This area has a relatively high-density of housing and many underground sites (abandoned mines and some caves), where bats can find suitable summer roosts and underground swarming and hibernation sites, respectively.

Different aspects of bat behavior in maternity colony roosts and in swarming sites were studied between 2000 and 2012. We studied population and genetic structure, social behavior, and the vocalization of swarming bats and colonies. Maternity colonies of *P. auritus* were located in the attics of buildings and tree hollows by means of radio-tracking or inspecting the buildings. Swarming sites for this species were found in known hibernacula and in city parks by netting and acoustic detection of audible *P. auritus* social calls.

Visits to summer roosts were made regularly in the villages of Stolec (Sudetic Foreland) and Krajanów (Sudety Mts.), approximately every 2–4 weeks in 2003 (Stolec) and in 2006 and 2010–2011 (Krajanów). One or two surveys were also conducted in Krajanów, also in 2001–2002, 2007, 2009, and 2012. The remaining roosts were checked irregularly or only once. The roost in Stolec village was found in the attic of a big house and in Krajanów in the church attic. The remaining roosts were located either in the attics of houses or churches or in tree hollows (Table 1).

Swarming sites in the Skałki Stoleckie mine (Sudetic Foreland) and the Gontowa mine (Sudety Mts.) were studied regularly between 2000 and 2003, once a week in March–April and August–October and every 2 or 3 weeks between May and the middle of August (Furmankiewicz 2008). The Szklary mines (Sudetic Foreland) were studied irregularly in 2003. Some behavioral studies were also performed in the Skałki Stoleckie mine and the Północna cave (Sudety Mts.) in 2008 (Maryjowski 2009) and in the Gilów mine (Sudetic Foreland), the Cieszków cellar (Silesian Lowland), and the Szachownica cave (Wieluń Upland) in 2009. Spring swarming activity was also observed in city parks in Wrocław, once a week in March–April in Szczytnicki Park and irregularly in Wschodni Park.

To examine the use of swarming sites as hibernation sites, we visited several hibernacula. Visits to the most intensively studied bat hibernacula (Skałki Stoleckie mine and Gontowa mine) were conducted in 2000–2003, every month between October and April (Furmankiewicz and Górniak 2002).

Bats were captured using mist-nets and a homemade small harp trap (about 0.5 × 1 m). The trap was used for catching bats at tree hollows. Bats were sexed, aged, and their forearm length and weight was measured. The reproductive status of the *P. auritus* was estimated on the basis of female nipples and male testes and cauda epididymides development (Furmankiewicz et al. 2013). Bats were marked with 2.9 mm aluminum bands (Fledermausmarkierungzentrale Dresden, Sächsisches

Landesamt für Umwelt und Geologie, Germany). In the colony in Krajanów, village bats were also marked with PIT tags (Trovan Ltd., United Kingdom) between 2009 and 2012. The circle antenna for the PIT tags (diameter 26 cm) were fixed to the colony entrance (see next paragraph) and connected with the reader (Dorset Group B. V., Aalten, Netherlands), which read and stored data about the time and ID of the bats passing through the antenna. This method enabled us to obtain a more reliable and detailed data set without disturbing bats by using mist-netting. However, some of the PIT tags of passing bats were not activated by the antenna, due to the high speed flight of the bats. Therefore, a tunnel around 25 cm long was made from a thin sheet of cork and was fixed on each side of the antenna, to slow down passing bats. This procedure helped, but still a few bats were missed; however, the data was reliable enough to get a monthly pattern of bat presence in the colony roost and the associations of bats emerging from and returning to the roost. Data from marked bats were used to evaluate the size of the populations (swarming and maternity colonies), the number of individuals in the colony roosts and swarming sites, the sex and age ratio, natal dispersion, and site fidelity (Furmankiewicz 2008; J. Furmankewicz, unpublished).

The number of individuals in the colony and the emergence and arrivals were estimated using custom-made frame with infrared diodes at the Krajanów roost between 2007 and 2009. It consisted of two lines of infrared diodes and recorded the time and direction of bat passes. Direction was estimated based on information about which line of the diodes was crossed by the bat first. The data did not contain information about bat identity. This device was fixed at the colony entrance. The colony entrance was located in one of the windows of the church tower. The remaining windows were covered by net to prevent the bats from using another entrance. This net was left in place for the study of bat activity by means of both PIT tag antenna and an infrared frame.

Twenty-six bats caught during swarming in the Skałki Stoleckie mine were radio-tracked to discover their day roosts around the swarming site and describe their activity and visitation frequency to the swarming site (Furmankiewicz 2008).

Genetic analysis was performed on (1) populations of bats swarming in the Skałki Stoleckie mine and the Szklary mine and (2) summer populations found by radio-tracking, members of which swarmed in the Skałki Stoleckie mine. One-wing membrane biopsy was taken from each individual as a DNA sample. DNA isolation, the dinucleotide microsatellite markers used, and details of the genetic analysis were described in Furmankiewicz and Altringham (2007).

Bat behavior, both in maternity colonies and at the swarming sites, was described using visual and acoustic methods. Flight behavior was recorded using CCTV and an infrared DVD camera DCR-DVD405 (Sony Corporation, Tokyo, Japan). Vocal activity patterns and vocal repertoire were recorded using a Pettersson D240x ultrasound detector (Pettersson Elektronik AB, Uppsala, Sweden) connected to a MP3 recorder and a condenser CM16 ultrasound microphone, with a Avisoft UltraSoundGate416 base unit connected to a laptop computer running Avisoft Recorder hardware (Avisoft Bioacoustics, Berlin, Germany) (Furmankiewicz 2004b, J. Furmankiewicz and G. Jones, in preparation). The sound files were analyzed using Avisoft-SASLab Pro version 4.40 (Avisoft Bioacoustics, Berlin, Germany) and Cool Edit Pro version 1.2a (Syntrillium Software Corporation, Phoenix, USA).

The functions of bat vocalizations were examined by a series of playback experiments. This study was conducted at four maternity colony roosts (Bożnowice, Jabłów, Krajanów, Muszkowice forest) in August and September 2008 and 2009 (J. Furmankiewicz and G. Jones, in preparation) and at eight swarming sites (six underground sites: Skałki Stoleckie mine, Gontowa mine, Szklary mine, Gilów mine, Cieszków cellar, Szachownica cave; and 2 city parks in Wrocław: Szczytnicki Park and Wschodni Park) in March and April 2009. At each maternity colony, we performed three or four playback experiments outside the roosts. At each swarming site, the playback was done twice (Skałki Stoleckie mine and Szachownica cave) or once (the remaining sites). Each playback session was performed on a different night. In the Gilów, Gontowa, and Szklary mines playbacks were performed only outside the mine, up to 50 m from the mine entrance. At the remaining underground sites, playbacks were conducted both outside and inside the site. In the city park they were carried out at a clearing, at spots where many vocalizations by *P. auritus* had been observed in previous years.

We used long original sequences of bat calls (as a test) and background noise from our recordings (as a control) to prepare broadcasted files. At swarming sites we broadcasted social calls recorded from the swarming population in the Skałki Stoleckie mine and at Szczytnicki Park in Wrocław. For the playbacks outside and inside the swarming sites, we used only the calls recorded outside and inside the swarming site, respectively. At the maternity roosts, we played back calls using recordings made in the roost of the colony where the experiments were being conducted, except for the Muszkowice forest where we used a file from the nearest colony in Bożnowice (J. Furmankiewicz and G. Jones, in preparation).

At each swarming site the file was played back for 30 min in total, in 5 min bouts of social calls and noise. The social calls were alternated with noise every 5 min, giving 15 min of social calls and 15 min of noise in total. The playback sessions started about 1.5 h after sunset outside the mine and afterwards were repeated inside the mine. This was the time of the highest bat activity at swarming sites (Furmankiewicz 2004a). In the colony roosts, the experimental sessions started 1 h before sunrise, i.e., when most colony members return to the roost, and we played back the files for 1 h following a schedule of 20 min calls, 10 min noise, 20 min calls, and 10 min noise (J. Furmankiewicz and G. Jones, in preparation).

The files containing calls of bats and control noise were played back at a sampling rate of 250 kHz via a Data Acquisition Card (National Instrument USB-6259 M series, National Instrument Corporation, Austin, TX, USA) using a Avisoft Recorder on a laptop connected to custom-made ultrasound amplifiers and Scan-Speak R2904 ultrasound loudspeakers (Scan-Speak, Videbæk, Denmark). The loudspeaker was fixed upward at the swarming sites, around 1 m height above the ground on a tripod. At colony locations we used two loudspeakers, fixed at 180° to each other, to increase the sound coverage.

Bat responses were recorded using infrared cameras (Sony Corporation, Tokyo, Japan) and a Pettersson D230 detector and then analyzed using the computer software mentioned above. There was 1 camera with 1 illuminator at each playback point. The cameras were placed about 10 m from the speakers, directed toward them, and fixed on tripods 1–1.2 m from the ground. The microphones were placed on the same tripods as the cameras about 1 m from the ground and directed at the speaker. Flight responses were classified into two categories: inspection flight (bats flying around and up to the speakers) and bat passes (bats passing through the visual field of the camera and not inspecting the speakers).

Bats were disturbed, caught, marked (ringed, radio-tracked, and PIT-tagged), and punched for biopsies under the licenses of local the Ethical Committee, Polish Ministry of Environment, and the local and main Environment Protection Agency.

2.3 Year-Round Activity, Size, and Composition of Different Functional Groups

2.3.1 The Year-Round Activity in a Nutshell

P. auritus forms social groups of different sizes and sex and age composition throughout the year, except in winter when they usually hibernate solitarily (Furmankiewicz and Górniak 2002). The annual cycle of this species can be divided into the following three phases: period with maternity colonies (from spring to autumn), spring and autumn mating period with swarming populations at underground hibernation sites, and winter hibernation. This concise scheme is similar to other temperate zone bat species, except for three main differences: (1) the length of the occupancy of summer roosts by maternity colonies is longer than in other species, (2) some males are residents in colonies throughout the whole summer season, and (3) the swarming period at underground sites is biphasic and takes place in spring and autumn, whereas in other swarming species it is an autumn phenomenon (Furmankiewicz et al. 2013).

2.3.2 The Size and Seasonal Changes in the Colony Number and Composition

Between April and June, the size of the maternity colonies of *P. auritus* in SW Poland varied from 2 adult individuals in tree hollows to up to 20–30 adults in buildings. The maximum number of bats observed in tree cavities was 8 and the minimum value for attics in buildings was between 3 and 5 individuals. We assumed that small groups of 2–5 individuals were a colony, because they were caught in roosts where more bats (bigger groups) were observed during other surveys. In July–September, when the young appeared in the colony, the attic dwelling colonies consisted of a maximum of around 40 individuals (data combined

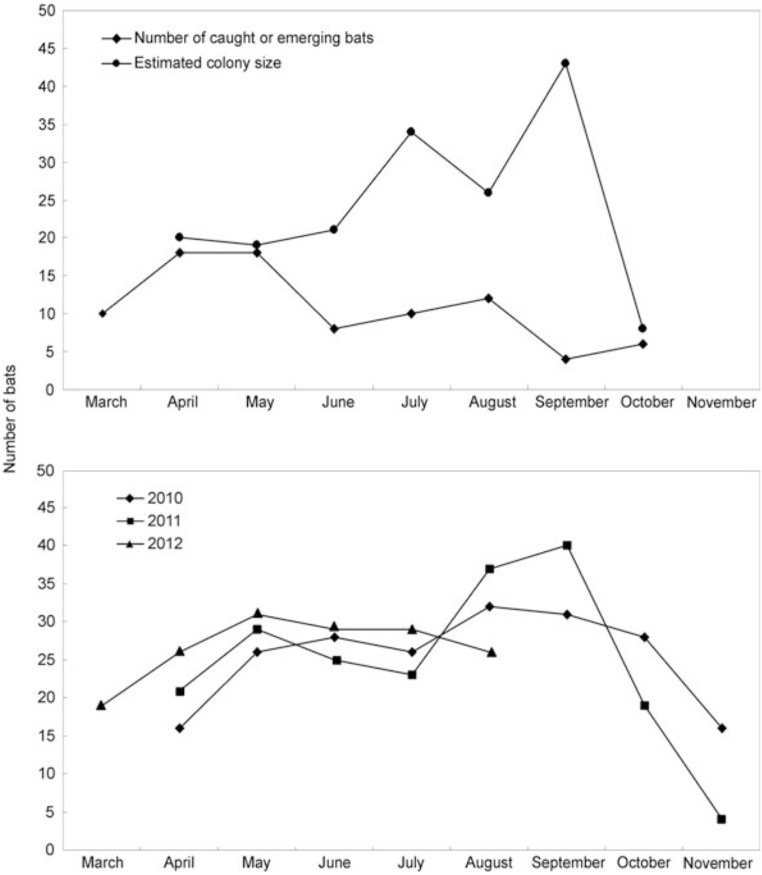


Fig. 2.1 Seasonal changes in the number of bats observed in the maternity colony roosts in Stolec (2003) and Krajanów (2010–2012), based on the number of emerging and caught bats (Stolec) and data from the PIT tag reader (Krajanów)

from PIT tag reader and calculation of the Jolly-Seber method, based on recaptures of banded bats) (Fig. 2.1).

The maternity colonies of *P. auritus* inhabited their roosts from March until November. Visual observations, mist-netting, and PIT tags confirmed the presence of bats in two of the most intensively studied colony roosts at this time of the year; however, only PIT tagging in Krajanów revealed that the bats were active in the maternity roost from the beginning of March until the end of November (Fig. 2.1), leaving the roost in the night, probably to forage. Nonetheless, activity and number of bats in the colony was low (a few individuals) before the 17th of March and after the 10th of November. The number of bats present in the colony gradually increased from March to April until May and then was stable until July, when the young bats appeared. The highest number of bats in the Krajanów colony was noted between July and September, and this number decreased in October (Fig. 2.1), probably due to both adult and young individuals leaving the roost.

The number of bats in the colony roost varied from night to night. Eighty bats (48 females and 32 males) were PIT tagged in total at the roost in Krajanów within the four seasons between 2009 and 2012. However, not every PIT tagged bat was recorded by the reader in this roost every night. This was partly a result of the inaccuracy of the PIT tag reader. However, bats may have also used other roosts in the vicinity, i.e., in the same village, and switched roost from time to time. There are no other known roosts in Krajanów, but in other study sites we recorded such movement during irregular studies. In Bożnowice village, bats used three roosts and there were two switches between them observed within one autumn season. In Bobolice and Jeszkotle, two individuals used tree holes and buildings and in the Muszkowice forest one bat switched between two tree holes. All those roosts were within a maximum of 1 km of each other (Furmankiewicz 2004a). Therefore, a maternity colony may be split into several roosts, inhabited by subgroups; however, the mechanism of splitting and roost switching was not studied.

It is not known if bats stay in their roosts through winter, but it is highly likely, as this species prefers a low air temperature and humidity in winter sites (reviewed in Swift 1998). The roosts had many crevices and holes in the wooden construction of the attics or in the walls, where bats could presumably hide and survive winter in a stable temperature and humidity. This species may also spend winter in tree hollows (Swift 1998), so it is highly likely that attics are also chosen as winter sites. On the other hand, *P. auritus* appears late in the hibernacula in the study area, at the end of November and in December, and disappears in March (Furmankiewicz and Górniak 2002). These dates coincide with the time when bats are no longer active in the colony before winter and the period when they appear again in the roost in the spring.

2.3.3 Sex and Age Composition of Maternity Colonies

The maternity colonies of *P. auritus* were composed of both adult females and adult males. The presence of males in the maternity colonies of this species is unique among European bat species and was also noted in other parts of Europe (Stebbings 1966; Heise and Schmidt 1988; Boyd and Stebbings 1989; Howard 1995; Entwistle et al. 2000); however, our results from the most intensively studied colony in Krajanów revealed that a stable number of resident and faithful males was present in the colony throughout the whole active season, i.e., from March until November (see below). The males constituted a relatively high proportion of the colony, which varied between 1 and 0 in Stolec and 0.2 and 0.5 in Krajanów in different months (Fig. 2.2). In the remaining roosts, the proportion of males varied between 0 and 0.86 (Table 2.1).

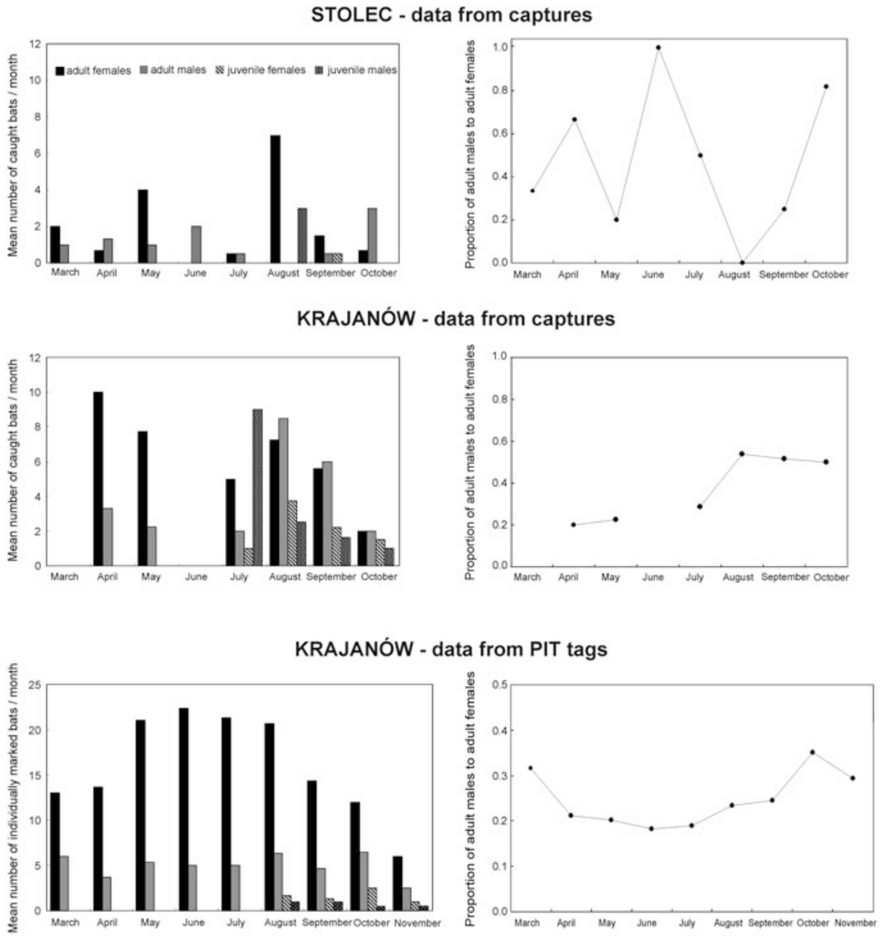


Fig. 2.2 The changes in number and composition of two of the most intensively studied maternity colonies of *P. auritus* caught in attic roosts in Stolec (2002–2003) and Krajanów (regularly in 2006 and 2010–2012 and occasionally in 2001–2002, 2007 and 2009). Data obtained by mist-netting and PIT tagging. Bats were not mist-netted in March and June in Krajanów. *M ad* adult males, *F juv/subad* juvenies/subadult females, *M juv/subad* juvenies/subadult males

Data collected in Stolec seem to be less reliable, probably due to a lower catching success, which was the only method for assessing the composition of this colony. The same seems to be true for the catching data from the Krajanów roost. Data obtained from PIT tagged bats in this colony showed different patterns. Individually marked bats, recorded at least once in a particular month by the PIT tag reader, are shown in Fig. 2.2. The number of adult males was stable between March and October, decreasing in November, but the proportion of males increased in October, November, and March, as a result of a lower number of females in those months (Fig. 2.2). These different patterns show the primacy of PIT tagging over

Table 2.1 The sex ratio of *P. auritus* in the less well-studied colonies in SW Poland in 2001–2007 (partly published in Duma et al. 2004)

Locality	Month	Number of catches in locality	Total number of adult females captured	Total number of adult males captured	Proportion of males
Bobolice	September	2	3	1	0.25
Bożnowice	July	1	14		0.00
	September	1	19	3	0.14
Góra św. Anny near Nowa Ruda	July	1	7	5	0.42
Henryków	August	2	1	1	0.50
	September	2	5		0.00
	October	2	7	1	0.13
Jabłów	August	1	14	6	0.30
Jeszkotle	October	2	6	4	0.40
Muszkowice, tree holes	August	1	1	1	0.50
	September	4	5	5	0.50
	October	1	9	9	0.50
Przygórze	August	1	7	4	0.36
Stolec, tree hole	October	2	7	5	0.42
Walim	July	1	1	6	0.86
Wolibórz	July	1	20	7	0.26
	August	1	15	1	0.06

Individuals caught more than once were shown here only once. All sites, except for Stolec and Muszkowice, were in the attics of big buildings, such as churches, monasteries, and palaces

mist-netting, which is more invasive and less accurate. This result also indicates that we must be cautious with the interpretation of data obtained using mist-netting and capture-recapture methods.

Young bats were caught in July or August, depending on the time of the survey. The proportion of juveniles to adult females varied between 0.1 and 0.3 (Krajanów, PIT tags), 2.0 and 0.7 (Krajanów, mist-netting), and 0.3 and 0.4 (Stolec, mist-netting) (Fig. 2.2). High values indicate that not all adults were caught, and very low values suggest a low capture success for juveniles or false age identification.

2.3.4 *Site Fidelity and Natal Dispersion in Colonies*

These habits were estimated only for the Krajanów roost, where long-term data (12 years) were available. The vast majority of bats were faithful to the roost within and between seasons. Twenty-seven (79.4 %) of the resident females and eight (100 %) of the resident males were noted in the colony for more than two years.

The number and composition of adult females was stable in every month from May till September in 2010–2012, when most of the individually marked females (92.1 %, $n = 35$) were always present in the colony; however, among those females 85.3 % ($n = 29$) were recorded every month and 17.7 % ($n = 6$) were absent in one or four months. The remaining females were noted only occasionally in one or two months (7.9 %, $n = 3$). In males, 50 % were residents in the colony and 50 % were observed only in one or two months, between August and October. Among the resident males, 62.5 % were observed in every month and 37.5 % were missing in 1–4 months. Such individuals may not have been recorded by the PIT tag reader and/or used other roosts in the vicinity, as discussed above for other sites. Individuals, who were recorded only during one or two months, may have visited the colony occasionally or might be juveniles who left the colony due to natal dispersion. False age identification of bats, which is possible in September and October, may have led to such biased data. Nevertheless, these results show the high stability of colony composition, which suggests that resident females and resident males of *P. auritus* form stable close colonies, with no or little movement between them. Natal dispersion was higher in males than in females. Among juvenile individuals, 50 % of young females and 80 % of young males disappeared from the Krajanów colony after the year of their birth. The remaining individuals stayed in the natal colony roost.

The stability of a colony can be strengthened by the longevity of this species. Several long living individuals were recorded in the Krajanów roost, for example one adult male who lived for at least 11 years (caught in 2001 and for the last time in 2012), one adult female who was at least 10-years old, and one adult female and two adult males that were at least eight years old. The remaining available data were as follows: two adult females that were at least five years old and three juveniles, three adult females, and one adult male that were at least four years old. The average life expectancy for most of the individuals was presumably lower, as the minimum estimates for the life expectancy of this species are 2.33 and 2.78 for females and males, respectively; however, those values may be overestimations due to low capture effort in some years (Burland et al. 2006).

2.3.5 The Size and Seasonal Changes in the Activity of Swarming Populations at Underground Sites

P. auritus swarms in underground sites, where it also hibernates. An intensive study of this behavior was carried out at the Skałki Stoleckie mine and the Gontowa mine in SW Poland (Furmankiewicz and Górniak 2002; Furmankiewicz and Altringham 2007; Furmankiewicz 2008; Furmankiewicz et al. 2013). Swarming activity was defined as when several individuals per night were caught and observed chasing and flying in and out of the mines. Subterranean swarming of *P. auritus* was recorded twice a year, in late summer/autumn (mid-August to mid-October) before hibernation and in spring (March–April) after hibernation. Few bats visited the mines outside of these times (Furmankiewicz and Górniak 2002; Furmankiewicz 2008).

At the Skałki Stoleckie mine (367 m a.s.l.), the first bats were caught in mid-February, but swarming started in the second week of March and lasted until the middle of April (Fig. 2.3). At the higher elevation Gontowa mine (640 m a.s.l.), swarming occurred approximately two weeks later and lasted until the middle of April, which was a result of a longer winter and hibernation. The beginning of early spring, defined as when the mean day and night temperature is 0–5 °C (Piasecki 1997), coincided with decreased numbers of hibernating bats and the beginning of spring swarming activity. Therefore, the pattern of swarming could be modified by local climatic conditions (Furmankiewicz 2004a, 2008). The autumn swarming activity at both mines peaked at the turn of August/September and lasted 7–10 weeks (Fig. 2.3) (Furmankiewicz 2008).

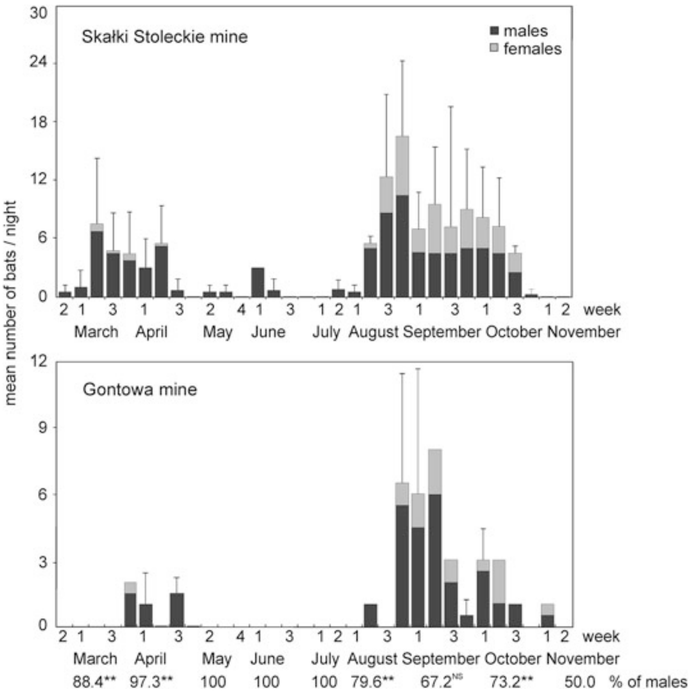


Fig. 2.3 Mean ± SD number of swarming *P. auritus* caught at the Skałki Stoleckie (2000–2003) and Gontowa (2000–2001) mines. Each column represents one to seven (1–2 only for May–July and November) or one to two nights for the Skałki Stoleckie and Gontowa mines, respectively. At Skałki Stoleckie we sampled every week, whereas we sampled from 4/III to 4/IV and from 2/VIII to 1/XI at Gontowa. The total monthly proportion of males at both sites and the level of significance (testing for significant departure from a 1:1 sex ratio, *NS* not significant, $*P < 0.05$, $**P < 0.001$, $***P < 0.001$, Friedmann ANOVA) are given below the *X*-axis labels. From Furmankiewicz (2008) with permission from Canadian Science Publishing

Autumn and spring swarming differed in terms of the number of individuals and the length of the swarming period, with smaller values in spring (Fig. 2.3). The length of the swarming activity also differed between sexes. Assuming that swarming involves at least a few individuals, males swarmed both in spring and in autumn, whereas females only swarmed in autumn. The very low number of females in spring suggests that they were only just leaving the hibernacula after arousal from hibernation, presumably to locate warmer summer roosts to facilitate gestation. Males were active at both mines for about two weeks longer than females, probably waiting for the first and last females. Single males were caught one week before the first females appeared, and one week after the last females had been caught (Fig. 2.3), but these data were not sufficient for statistical testing. Males probably do not remain at the hibernacula, as some of them were observed in their day roosts around the swarming site at this time of year (Furmankiewicz 2004a).

The estimation of population sizes was based on 88 recaptures from 233 banded bats, using the Jolly-Seber method. The total swarming population size at Skałki Stoleckie was 492 individuals (417–567, 95 % confidence interval CI). The autumn population [2001 = 338 (189–487, 95 % CI), 2002 = 230 (151–309)] was 25–40 % greater than in spring [2001 = 271 (119–423), 2002 = 201 (107–299), 2003 = 175 (46–304)] when comparing autumn with the following spring (e.g. autumn 2001 with spring 2002) (Furmankiewicz 2008). It was not possible to estimate the population size of the Gontowa mine, due to the smaller sample; however, the number of captured bats was around two times smaller than the population in the Skałki Stoleckie mine (Fig. 2.3). However, swarms visiting individual sites may be larger, as there was a high turnover of individuals from night to night, so the recapture rates on consecutive nights could be low.

2.3.6 Nocturnal Activity in Underground Sites

More individuals were caught during the first half of the night in spring, with a high number of males in the first hour after sunset. In autumn, activity became higher and higher as the night progressed and most individuals were recorded between 3 and 6 h after sunset (Furmankiewicz 2008).

The activity of radio-tracked bats revealed that some stayed at the Skałki Stoleckie swarming site for 2–3 h (two radio-tracked males in spring and one female in autumn) after release and before returning to a day roost. Those bats flew in and around the mine emitting social calls and landing from time to time on a rock wall or tree branch. They also returned to the mine within 1–3 days from roosts located between 0.5 and 11 km from the swarming site. Other bats (a male in spring and a female in autumn) stayed at the swarming site, the whole night after release and throughout the next day. They left the mine at the beginning of the next night, after which they became active. The male was lost but the female went to a nursery roost 31.5 km away (Furmankiewicz 2004a, 2008).

2.3.7 Sex and Age Ratio of Swarming Bats

Depending on the site and season, 85.7–94.1 % of swarming bats were classified as adult, but the number of subadult individuals may be underestimated due to the limitations of the age determination method at this time of the year. The swarming population was strongly male biased. Males significantly outnumbered females during the spring and autumn swarming periods. The lowest proportion of females occurred in spring (0.09 at Skałki Stoleckie and 0.13 at Gonotwa) and none were caught in summer. More females visited the mines in autumn than in spring, and the proportion increased in mid-September and mid-October, when the sex ratios were 0.52 and 0.4, respectively at the Skałki Stoleckie mine and 0.33 and 0.4, respectively at the Gontowa mine (Figs. 2.3 and 2.4) (Furmankiewicz 2004a, 2008).

2.3.8 Visitation Frequency and Fidelity to Swarming Sites

More bats of both sexes were recovered during swarming (37.8 %, $n = 88$) than during hibernation (1.3 %, $n = 3$). However, both sexes showed different visitation frequencies and fidelity to swarming sites. At the most intensively studied swarming site at Skałki Stoleckie the data set was big enough (233 banded bats, 170 males and 63 females within 3 seasons) to compute those estimates. Males were more prone to visit swarming sites more frequently and showed higher fidelity to swarming sites than females. Overall 36.1 % of males visited the mine only in autumn and 49.2 % both in spring and autumn, the remaining males were recorded

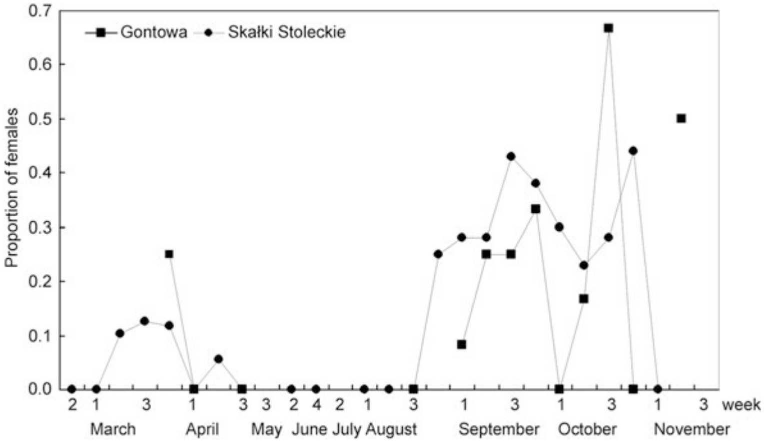


Fig. 2.4 Seasonal changes in the sex ratios (females to males) of swarming populations in the two most intensively studied swarming sites in SW Poland: Gontowa mine (2000–2001) and Skałki Stoleckie mine (2000–2002)

only in spring. In contrast, most females visited the mine only in the autumn and there were no females that visited the mine only in spring (Furmankiewicz 2008).

In total 17.6 % of all bats caught were captured at least twice in a season and rarely 3 or 4 times; however, the sampling rate (once a week) could be too rare to detect more visits: therefore, it is possible that some of the swarming bats came to the mine more than twice. However, on six occasions netting was carried out on 2 or 3 consecutive nights and no recaptures from the first night were recorded (Furmankiewicz 2008). More males revisited the swarming site than females (17.6 % vs. 12.7 % of banded males and females respectively). The mean number of days between recaptures for males was significantly lower in spring (14.1 days, range = 1–41, SD = 11.8, $n = 11$) than in autumn (27.1 days, range = 3–49, SD = 14.8, $n = 19$). Females revisited the mine in autumn (9.9 days, range = 3–24, SD = 8.1, $n = 11$) more frequently than males (Furmankiewicz 2008).

Long-term fidelity to the Skałki Stoleckie swarming site was shown by the recapture in one of the following seasons (spring 2001–autumn 2003) of 48.6 % of bats banded in autumn 2000; however, there were more recaptures for males (55.8 %) than for females (31.8 %). Moreover, bats seemed to be faithful to one swarming site, as we never caught bats from the Skałki Stoleckie mine at another swarming site in the vicinity during swarming time and radio-tracked bats did not visit other swarming sites (Furmankiewicz 2004), which might suggest low gene flow between swarming sites.

2.3.9 Day Roosts of Swarming Bats

Data on the type and distance of the daily roosts of swarming bats were collected at the Skałki Stoleckie mine by radio-tracking 24 bats caught swarming at this site. These roosts were used by at least 36 individuals (17 males and 19 females) known to swarm at Skałki Stoleckie, based on banded bats observed in the colonies. Roosts were located between 0.5 to 31.5 km NE and E of the mine (Fig. 2.5). Males roosted closer to the swarming site than females (Fig. 2.5). The minimum–maximum distance between the day roost and the swarming site for males was 0.5–6.5 km (mean ± SD 3.1 ± 1.8 km) with no difference between spring and autumn roosts, and for females 1.5–31.5 km (mean ± SD 8.9 ± 8 km). Therefore, the minimum convex polygons encompassing all the roosts of each tagged bat were larger for females than for males, 93 and 14.5 km^2 respectively (Furmankiewicz 2008). It is highly likely that the home area of swarming bats is greater than that uncovered, as the highest known distance between the summer and winter roosts of *P. auritus* is 88 km (Gaisler et al. 2003).

The swarming site at Skałki Stoleckie was visited by solitary males and members of maternity colonies, both males and females. Bats roosted in tree holes (11 males and 10 females) and attics and crevices of buildings (9 males and 11 females). Roosts were inhabited by single males or maternity colonies (Furmankiewicz 2008). In spring, only males, who roosted solitarily, visited the mine ($n = 4$);

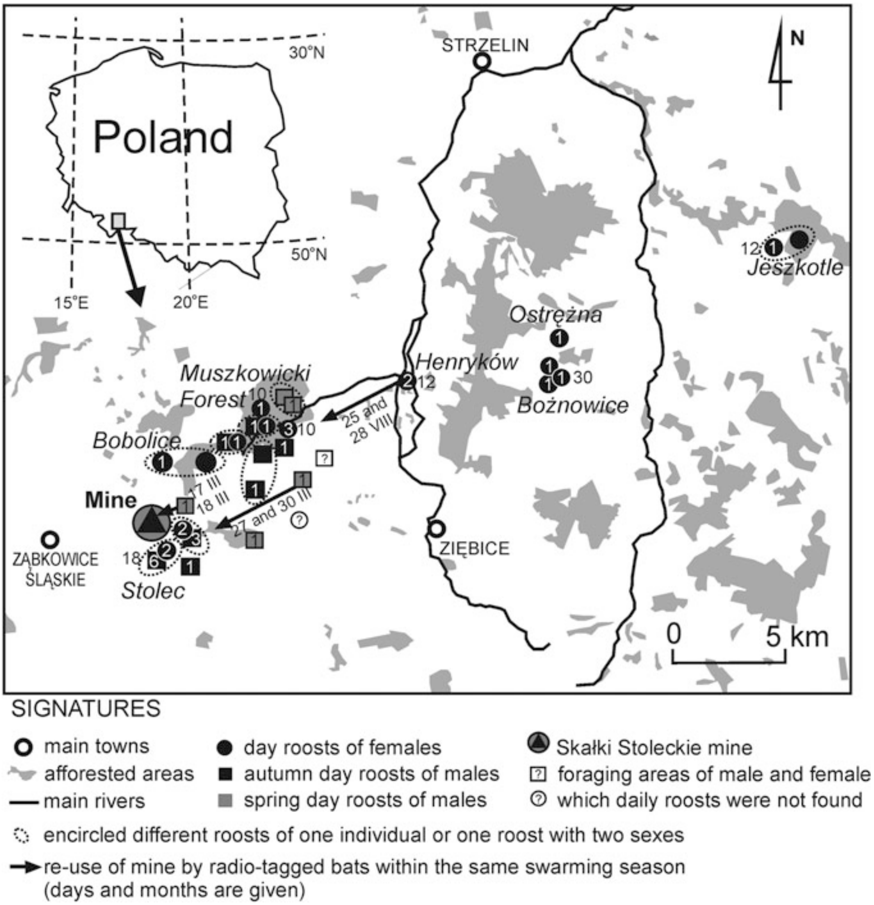


Fig. 2.5 Day roosts of *P. auritus* males and females caught during autumn and spring swarming at the Skałki Stoleckie mine. The number of swarming bats found at each roost is given in the *circle* and *square* figures. The most numerous shelters (≥10 individuals) are shown with the number of bats near the roosts marked (remaining roosts were inhabited by 1–8 individuals). From Furmankiewicz (2008) with permission from Canadian Science Publishing

however, there was one male who visited the mine in spring, and in June he was observed in a maternity colony in the nearest Stolec village. In autumn, there were two solitary males found to swarm in the mine and 10 males who came from maternity colonies (Stolec and Muszkowice) located up to 6 km from the swarming site. Three of those males seemed to be residents in the colonies, as they were recorded there 2–3 times between April and October; the remaining males were observed in the colony roosts only once (Furmankiewicz 2004a). These results suggest two strategies in males: solitary males visiting both maternity colonies (in autumn) and swarming sites (both in autumn and spring) and colony males spending their whole active period with females and also visiting swarming sites.

2.3.10 The Genetic Structure of Swarming Bats and Summer Colonies

We analyzed the genetic structure of swarming bats and bats from maternity colonies found to swarm at the Skałki Stoleckie mine (Furmankiewicz and Altringham 2007). The number of genotyped bats was 51 females and 60 males from the swarming site and 64 females and 38 males from the colonies. A group of more than one individual found within a single roost was considered as a colony. Bats sampled within a single village or a small forest area (about 500 ha) in all known roosts were considered to be a single summer population (Furmankiewicz and Altringham 2007). We made this simplified distinction to facilitate data presentation; however, we have no data to support this classification.

All summer and swarming populations showed similarly high gene diversity (H_s = 0.77) and heterozygosity (H_O = 0.75). Summer colonies showed a low level of inbreeding (F_{IS} = 0.017); however, some differentiation among summer colonies was recorded (F_{ST} = 0.024) (Furmankiewicz and Altringham 2007).

In summer colonies relatedness overall was low, but greater among females than males and female relatedness was significantly different from zero (colony females r = 0.059 and males r = 0.022). The relatedness of females in summer colonies was higher relative to swarming females (r = −0.31). The relatedness among males from both swarming sites (r = 0.11) and summer colonies was low and not significantly different from zero. Within-summer populations pairwise relatedness overall was low, but higher than between-summer populations (r = 0.029 and r = −0.019 respectively) and significantly different from simulated values. This was probably influenced by high values for females. The within-swarming population relatedness was very low and not different from the expected values (Furmankiewicz and Altringham 2007). Low inbreeding coefficients and low average relatedness in the summer colonies indicates high gene flow in maternity colonies.

There was no significant genetic isolation by distance for the colonies over a distance of 31 km (P = 0.697 or 0.829 depending on the number of loci used). There was also no significant increase in the genetic distance of summer population samples from the Skałki Stoleckie swarming site with geographical distance (regression, P = 0.442) (Furmankiewicz and Altringham 2007). Both these results again suggest gene flow between bats that swarm in underground sites.

Despite the detected gene flow between colonies, almost every pair of summer populations was significantly genetically different from each other; however, these genetic differentiations could be generated by female philopatry. Most of the summer populations were also significantly different from the Skałki Stoleckie swarming site, with the exception of the colonies from the roosts closest to the swarming site (up to 6 km). Moreover, there was a negative relationship between the distance from the Skałki Stoleckie mine to the summer colony, and the assignment of swarming bats to summer populations (r_s = −0.657, n = 6, NS), i.e., about 61 % of swarming bats were assigned to the three nearest summer populations: Bobolice, Stolec, and Muszkowice (see Fig. 2.5). There was also a negative relationship between the proportion of bats from each summer population assigned to the Skałki Stoleckie swarming site and the distance from the swarming site ($r_s = -0.6$ or $r_s = -0.429$ depending on number of loci analyzed, $n = 6$, NS). Those two estimates were not significantly correlated, but were confirmed by the movement of radio-tracked bats. More bats captured at swarming sites were radio-tracked to nearby summer roosts (Stolec and Muszkowice) than more distant roosts (Furmankiewicz 2008). This suggests that as distance from a particular swarming site increases, bats are more likely to use other sites closer to their roosts, but bats from one colony may visit more than one swarming site, facilitating limited gene flow between swarming sites. The last hypothesis is supported by the proportion of bats from each colony assigned to a swarming site, which ranged from 41–100 %. The proportion of individuals not assigned to a swarming site varied between 0 and 59 %. However, this may also indicate that not all colony members visit the swarming site (Furmankiewicz and Altringham 2007).

Overall, 26.5–28.6 % of the bats in the Skałki Stoleckie swarming population were not assigned to the sampled summer populations, which means that there were undiscovered summer populations (Furmankiewicz and Altringham 2007). The total swarming population size of *P. auritus* at this study site was estimated to be around 500 individuals (see above). The average size of a summer colony of this species amounts to around 30–50 individuals (this study, Entwistle et al. 2000). Therefore, swarming bats may come from at least 10 summer colonies or perhaps many more.

2.4 Behavior in Colonies and Swarming Sites

2.4.1 Flight Behavior and Social Calling in Maternity Colonies

The behavior of bats in maternity colonies was intensively studied at the colony in Krajanów, which inhabits the attic of the church. The attic is relatively big (about 30 m long and 10 m wide at floor level) and has a sloping roof at a height of around 6 m. Bats flew along the attic and vocalized before leaving the roost. During returns in the night or at dawn they behaved in a similar way. When the bats approached the roost entrance, both before departure and during arrival after foraging, some of them also vocalized. Occasionally, they also swarmed around the roost entrance and vocalized at dawn before they entered the roost. Dawn swarming with vocalizations around the roost was also observed in colonies in tree cavities. Dawn swarming lasted for around 20–40 min before the bats entered the tree hole or crevice in the attic (J. Furmankiewicz and G. Jones, in preparation, J. Furmankiewicz, unpublished).

Analysis of bat activity 1 h before their evening emergence and 1 h before sunrise over 7 nights during May, June, and August, revealed several different flight activities, including straight flight along the attic (36 % of the total activity), flight on wave-like trajectory (10 %), loop flight (half or full loop) (27 %), change of attic level (21 %), hovering (2 %), and other forms of flight activity (4 %) (Zieliński 2013). Around 10–16 % of bat activity involved tandem flights. Occasionally, bats flew in groups of up to 4 individuals. There were more tandem flights in the morning, during the arrival of most colony members, than during the evening before emergence. There were also more tandem flights in June and August than in May; however, this difference was not statistically significant (Zieliński 2013). This pattern presumably results from the activity of young bats, which may follow adults (in June) or participate in the total activity of the colony in August. Mating activity may also explain the tandem flights in August, as the mating period starts around this time of year and copulations can take place in colony roost (Stebbings 1966, 1970; Swift 1998). Similar patterns of tandem flights were also observed in a maternity colony in Jabłów (Przepiórka 2016), one of the villages used during playback experiments of social calls.

Data from the infrared frame fixed at the entrance of the colony also revealed group emergences and arrivals. Analysis was performed on the data of bats recorded by the infrared frame between July 18th and August 12th 2007. The remaining data are still currently being analyzed (Furmankiewicz et al., in preparation). A group was scored when two or more passes were recorded by the frame within a 2–10 s time window. In total around 28 % of individuals emerged and 38 % returned in pairs or sporadically in groups of 3–4. Data from individually marked bats, using PIT tags, revealed that there was no preference by any given individual to perform tandem flights more often with the same colony member during emerging from or returning to the colony roost, i.e., about 70 % of the combinations of pairs recorded by PIT tags were observed only once, 20 % were noted twice, 3.5 % on three occasions, and about 3.5 % four times, with one pair recorded six times. These associations were recorded between adults of both sexes (about 54 % between adult females and 34 % between adult males and females), and adults and young (about 10 % between adult females and young individuals and only one case between an adult male and a young male). There was also one pair of juvenile males and one pair of adult males. So it seems that bats join other members relatively randomly, independent of the sex and age.

Colony members emitted two types of social calls: audible single frequency-modulated calls and inaudible undulating calls (Fig. 2.6). The single calls were emitted singly or as a series of double, triple, or multiple calls inside the church attic when the bats were leaving and entering the roost at night or dawn or during the dawn swarming around the roost entrance (Furmankiewicz 2004b; J. Furmankiewicz and G. Jones, in preparation).

The recording of bat vocalizations was performed from April until October in 2006–2007, every 1–2 weeks. Vocalizations increased gradually from April to July, peaking in July and then again gradually decreasing (Fig. 2.7). The peak in July, and also relatively high activity in August, was probably related to the intense communication between mothers and their young or between young as they started to fly. The August peak may also be connected with mating behavior, as with the increase in the proportion of tandem flights in this part of the year (see above). The

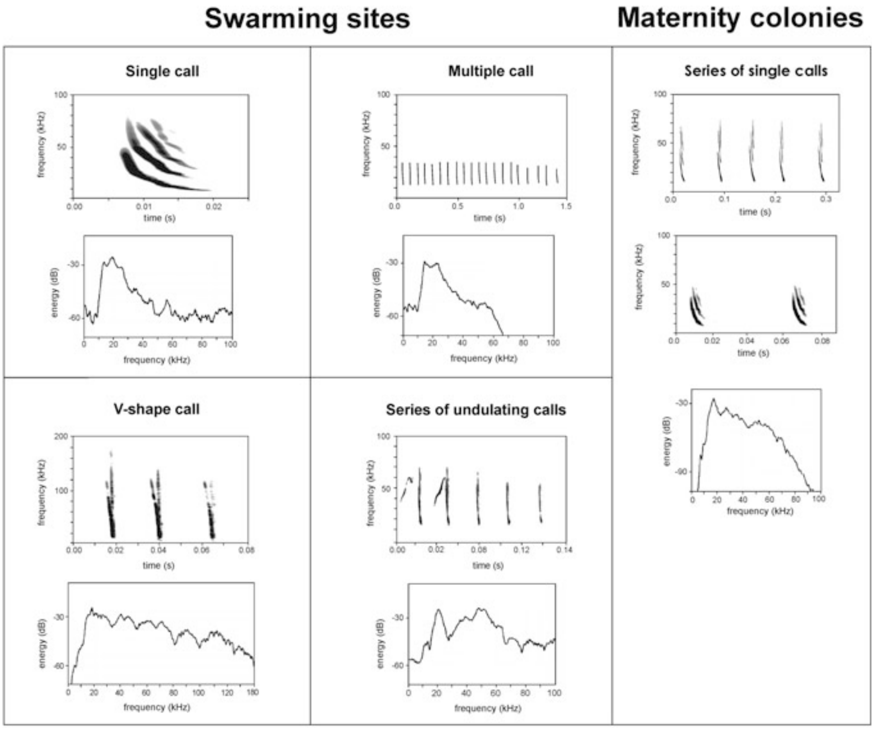


Fig. 2.6 The different types of social calls by *P. auritus*, recorded at swarming sites and maternity roosts. The *upper graphs* show spectrograms, while the *lower graphs* show power spectra. Adapted from Furmankiewicz et al. (2013) with permission from the Museum and Institute of Zoology, Polish Academy of Sciences

increase at the beginning and decrease at the end of the season appears to be a result of the growing and declining number of bats in the colony, respectively (see chapter 2.3.2). In August and September 2006–2007, returning bats emitted more social calls in the attic than emerging ones (Fig. 2.7). As males are also members of the colony, we may expect that they call as well. Therefore, it is very likely that calling in the colony roost involved adult members of both sexes and offspring. However, we have no direct evidence of this, but pairs of bats emerging from and arriving to the roost were observed to vocalize and those pairs involved both females and males.

Playback experiments of the social calls emitted by bats in the colony revealed the response of *P. auritus* to the calling of conspecifics, presumably of both sexes. The response involved investigation of the loudspeakers, by passing and by approaching them and flying around them, and sometimes the emission of social calls (J. Furmankiewicz and G. Jones, in preparation).

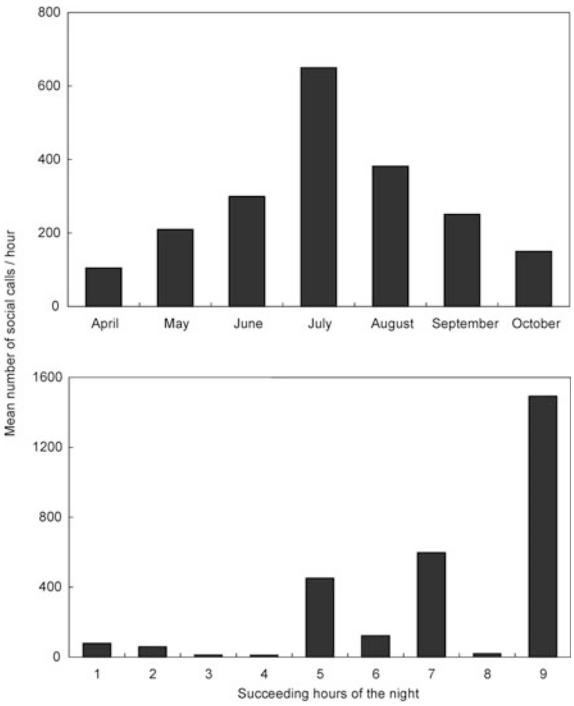


Fig. 2.7 Seasonal (2006) and overnight (August and September 2006–2007) changes in the vocal activity of *P. auritus* recorded inside the maternity roost in Krajanów in 2006. The succeeding hours of the night were as follows: first hour is an hour after sunset and ninth hour is an hour before sunrise

2.4.2 Flight Behavior and Vocalizations of Bat Swarms at Underground Sites

Videotaping with infrared light at two underground sites (Skałki Stoleckie mine, Północna cave) in autumn enabled us to classify bat behavior, but usually without identification of the species, as most of the swarming bats were similar in size and flying fast. At two studied swarming sites, eight bat species were recorded during swarming: *P. auritus*, the barbastelle *Barbastella barbastellus*, Natterer's bat *Myotis nattereri*, Daubenton's bat *Myotis daubentonii*, greater mouse-eared bat *Myotis myotis*, and Brandt's bat *Myotis brandtii*. In total 48.9 % of all the events were classified as they passes through the visual field of the camera in one direction, 34.3 % were looping flights, 13.3 % were classified as chases by two individuals, 1.6 % were chases of more than two individuals, and 1.9 % of bats landed on the rock walls (Maryjowski 2009; Furmankiewicz 2004b; Furmankiewicz et al. 2013).

The flight activity of swarming bats was accompanied by the emission of social calls. *P. auritus* emitted calls mainly in flight, but bats perched on a rock wall, tree trunk, or tree branch also produced social calls. Social calls were emitted near the entrances of the mines, as well as inside and outside the mines, although subterranean vocalizations were detected only at Skałki Stoleckie, where vocalizations were more intense inside than outside (Furmankiewicz 2004b).

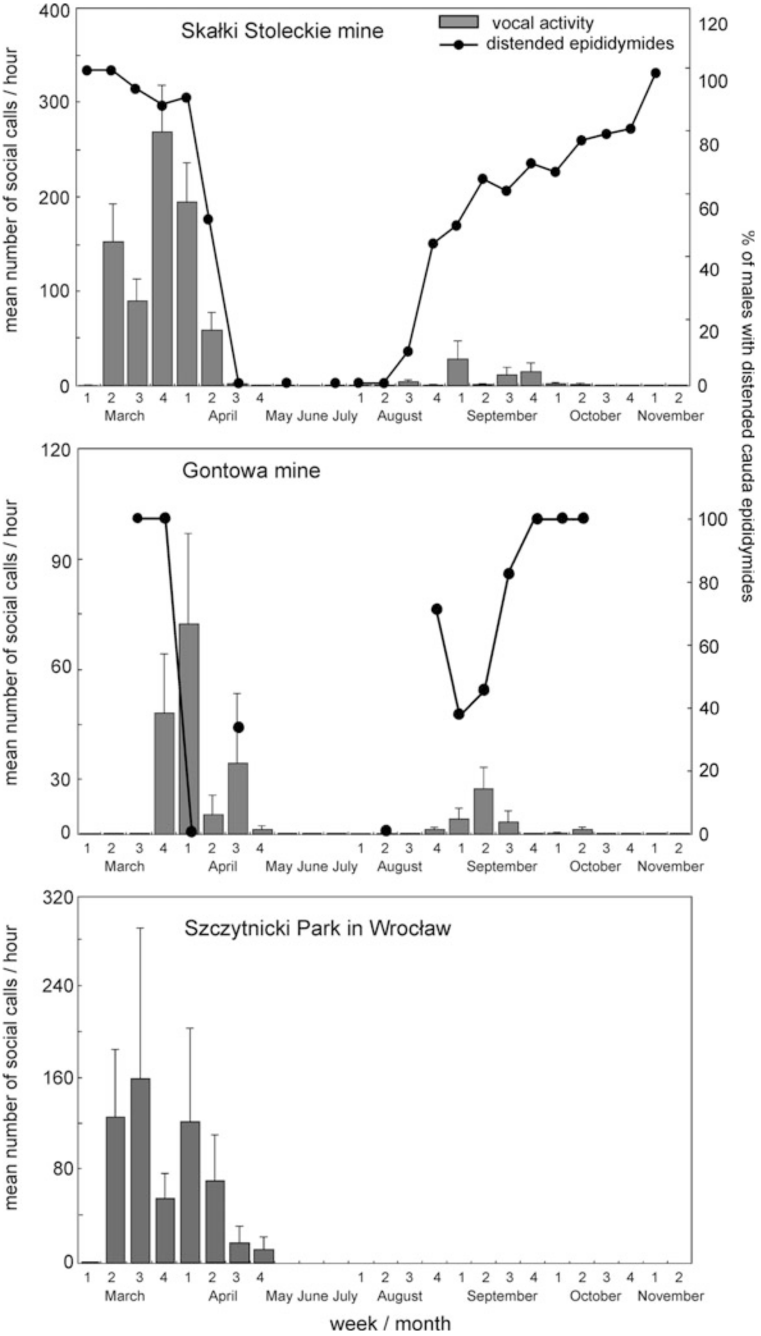
Five basic types of calls at the swarming sites were distinguished: single, double, multiple (long and rapid series of single calls), undulating, and V-shaped (Fig. 2.6). Except for the V-shaped calls, all calls were emitted both during songflight and perching. V-shaped calls were produced during chases of two or more individuals. Single calls were the most often produced (72 % of recorded social calls) and no other bat species is known to produce such signature calls. The remaining identified calls appeared between the echolocation calls of *P. auritus*. Single calls and undulating calls were similar in structure to those emitted by bats in the maternity colonies (Fig. 2.6); however, the single calls significantly differed on time and frequency parameters (Furmankiewicz 2004b). Therefore, we assume that all of the calls were emitted by this species.

Social calls emitted in autumn by swarming *P. auritus* constituted 6.3–13.3 % of vocalizations. The remaining calls were echolocations (Maryjowski 2009). However, the autumn (from mid-August until the end of October) vocal activity of *P. auritus* was around 10 times lower than in spring (i.e. from mid-March until mid-April, Fig. 2.8). No swarming or vocalizing bats were observed during the summer. Single calls were detected throughout the whole swarming season, while the other types of calls were recorded mainly in spring. The diversity of social calls produced by swarming bats was highest during the spring peak of vocalization activity (Furmankiewicz et al. 2013).

Spring vocal activity in *P. auritus* was also observed in the city parks of Wrocław (Fig. 2.8), but here no data on the number and sex ratio of bats were available. Bats made songflight displays between trees and above the park clearings, and vocalized while perching (on tree branches or tree trunk), mainly using single social calls (Furmankiewicz 2004a, b).

At Skałki Stoleckie, there was a significant positive correlation between vocalization intensity and the number of males caught. At Gontowa, this correlation was weaker and was not statistically significant. There was a positive correlation between vocal activity and the number of females captured at both mines, but this was only statistically significant during autumn at Gontowa. There was also a significant positive correlation between the vocal activity of *P. auritus* and the proportion of males with distended caudae epididymides at the Skałki Stoleckie swarming site (Furmankiewicz et al. 2013). When vocal activity peaked in spring, most of the males had distended caudae epididymides. In autumn, vocal activity was low, in spite of the fact that the proportion of males with distended caudae was relatively high (Fig. 2.8). The proportion of males with enlarged and distended caudae was highest in early spring (from the middle of March until the beginning of April) and in autumn (from the beginning of August until the end of October), both at swarming sites and maternity colony roosts; however, the area of caudae epididymides (length × width) was highest in spring (Furmankiewicz et al. 2013). The size of epididymis in spring indicates that males are capable of inseminating females at this time of year.

Playback experiments of social calls of swarming *P. auritus* revealed a strong significant response to played back social calls. Bats inspected the loudspeaker during the broadcast of social calls significantly more often than during noise emission


Skałki Stoleckie mine
vocal activity
distended epididymides
mean number of social calls / hour
% of males with distended cauda epididymides
400
300
200
100
0
120
100
80
60
40
20
0
Gontowa mine
120
90
60
30
0
100
80
60
40
20
0
Szczytnicki Park in Wrocław
320
240
160
80
0
1 2 3 4 1 2 3 4 1 2 3 4 1 2 3 4 1 2 3 4 1 2
March April May June July August September October November
week / month

◀ **Fig. 2.8** Seasonal changes in the vocal activity and proportion of male *P. auritus* with distended caudae epididymides observed at swarming sites. Means and standard errors are given for the vocal activity and the total proportion of males for 2000–2002 for the Skałki Stoleckie mine (n = 326 males) and for 2000 and 2001 for the Gontowa mine and the Szczytnicki Park in Wrocław (n = 45 males). All types of calls are included. No data on caudae epididymides was available for the city park and no vocalizations were observed in this park during autumn. Adapted from Furmankiewicz et al. (2013) with permission from the Museum and Institute of Zoology, Polish Academy of Sciences

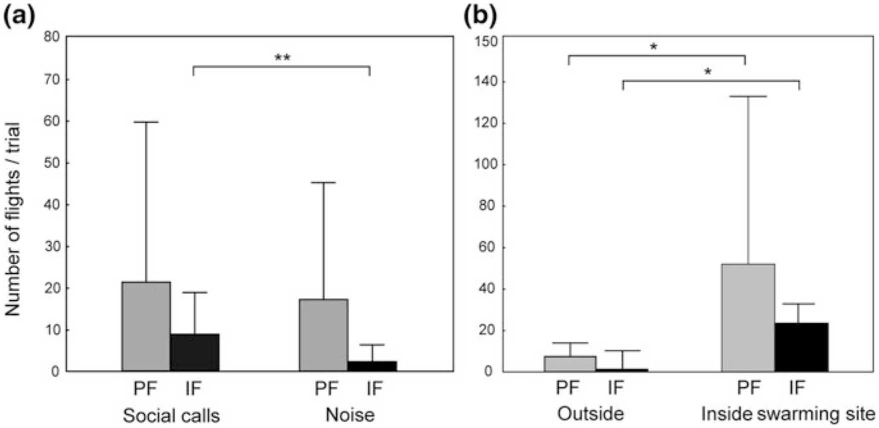


Fig. 2.9 Bat responses to playbacks of ‘spring’ social calls by *P. auritus* at underground swarming sites and in city parks (n = 14 trials). **a** all sites together, **b** response to social calls given outside and inside the Skałki Stoleckie mine and the Szachownica cave (n = 4 trials). *PF* passing flights, *IF* inspection flights. Median and minimum–maximum values are shown. The differences between playback sessions was tested with either Wilcoxon test (**a**) or Mann-Whitney test (**b**), $^{**}p < 0.001$, $^{*}p < 0.05$

(Wilcoxon test, n = 14, $Z = 2.599$, $P < 0.01$). The number of passes between social call sessions and noise sessions was not significantly different (Wilcoxon test, n = 14, $Z = 1.258$, NS) (Fig. 2.9). At the sites where playbacks were conducted inside and outside underground swarming sites (the Skałki Stoleckie mine and Szachownica cave), the response of bats to the social calls was stronger inside than outside (Mann-Whithney test; number of inspection flights: $Z = -2.4495$, $P < 0.05$; number of passes: $Z = -2.4495$, $P < 0.05$) (Fig. 2.9). Bats sometimes responded with social calls, but in such cases they usually did not fly up to the loudspeaker.

2.5 Conclusions

The social organization of *P. auritus* is complex and its social behavior diversifies depending on the time of year and type of bat aggregation (Fig. 2.10). Bats stay in mixed sex colonies throughout the whole active period; however, some males roost

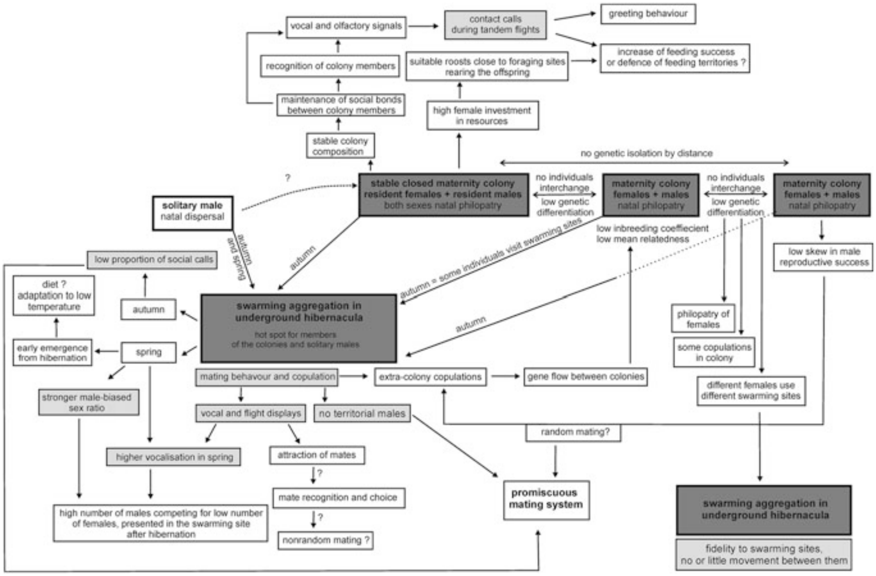


Fig. 2.10 Social organization of *P. auritus* with possible causes and consequences

solitarily. Both sexes are faithful to a colony within one season and over many years. Members of the colony use contact calls and some of them perform tandem flights during emerging from and returning to the colony roosts. Twice a year, in autumn and spring, members of the colonies and solitary males gather at swarming sites, where they make flight displays, which often involve vocalizations. Bats are also faithful to swarming sites. Fidelity to roosts and swarming sites, the stable composition of the small and closed colonies, probable longevity, communal breeding, and the similar objectives among group members (care for offspring, improvement of thermoregulation, food location and defense, and mating) has led to a complex social system with positive consequences (inbreeding avoidance and the maintenance of genetic diversity) for the population genetics of this species (Fig. 2.10). Ecological, physiological, and morphological factors, as well as the different strategies of the sexes, may explain the behavior and population organization of *P. auritus* (Fig. 2.10). The main general assumptions of this schematic pattern may be relevant for other temperate zone swarming species, as similar genetic consequences of swarming behavior and some similar organization in swarming and summer populations have been seen in these species (e.g. Kerth et al. 2003; Parsons and Jones 2003; Rivers et al. 2005, 2006; Kerth 2006).

It has been suggested that the temperate-zone climate and wing morphology are two of the main factors affecting the behavior and ecology of *P. auritus* (Burland et al. 2006). Individuals aggregate in a colony to keep warm, which is important especially for offspring in a variable temperate-zone climate. The presence of males in the colonies of *P. auritus* is rather unusual for a temperate bat species and so far has only been described in *P. auritus* (Horáček 1975; Park et al. 1998; Howard

1995; Entwistle et al. 2000; Burland et al. 2006; this study) and *M. daubentonii* (Senior et al. 2005). Resident males in a colony roost may increase the thermal benefits for colony members (Entwistle et al. 1996; Burland et al. 2006). However, a thermal explanation does not explain why some males roost solitarily (Furmankiewicz 2008). Such segregation among males was also described for *M. daubentonii*, where downstream males roost with females and, therefore, have access to good quality foraging sites and to females during the mating period. They also sire most of the juveniles in the nursery roost. In contrast, upstream males are excluded and roost together. They explore poor qualitSy habitats and have significantly lower mating success. Similarly, there were also a small proportion of potential fathers sampled at swarming sites (Senior et al. 2005). In *P. auritus* colony males fathered less than 20 % of the colony offspring (Burland et al. 1999). Moreover, both categories of males visited swarming sites; however, only males from colonies located close to the swarming sites were tracked (Furmankiewicz 2004a). Therefore, the factors affecting the different strategies of males might be diverse, e.g., interindividual variation in behavior, physiology, and thermal preferences of males (the use of either warmer roosts with females or colder sites without other bats), and the trade-off between longer distances to foraging sites and communal roosting or closer foraging habitats and solitary roosting in lower quality roosts. Additionally, competition for limited foraging sites close to colony roosts, may determine the size of the colony, including the number of males. Colony males exploit foraging grounds that are located further away from the colony than females (Entwistle et al. 1996), which could prevent competition for food resources between colony members (Burland et al. 2006); however, there might be a restricted number of foraging sites situated within an acceptable distance for everyday movement. Therefore, there is a balance between energetic (thermoregulation, shorter distance to foraging areas, etc.) benefits and losses, which may arise from the wing morphology of this species. The low wing loading and low aspect ratio in this species (Norberg and Rayner 1987) is assumed to result in short flight distances between roosts and foraging grounds, and hence small colony sizes (Entwistle et al. 2000; Burland and Worthington Wilmer 2001; Burland et al. 2006).

However, wing morphology constrains do not explain the frequent visitation of swarming sites from distant day roosts (Furmankiewicz 2008). Contrarily, this behavior emphasizes the importance of swarming sites and the swarming period, due to the high energy expenditure for the long flight to such a site. Swarming involves both members of different colonies and solitary males; therefore, swarming populations can be large (Parsons and Jones 2003; Rivers 2005; Furmankiewicz 2008). The maternity colonies of *P. auritus* are small, philopatric, and spatially isolated with little exchange of individuals (Burland et al. 1999; Entwistle et al. 2000); therefore, there is a high risk of inbreeding. However, colonies had high gene diversities, low colony relatedness and low inbreeding coefficients (Burland et al. 2001; Furmankiewicz and Altringham 2007), and a very low number of offspring sired by males from the same colony (Burland et al. 2001). This suggests copulations outside the colonies and high gene flow between summer colonies. One may expect mating in a site with a high number of bats, as traveling from one colony to another to find sexually active mates would be energetically expensive and might not completely reduce inbreeding risk. Hibernacula provide an ideal opportunity for extra-colony mating, as bats gather from many colonies during autumn and spring to swarm at one site (Kerth et al. 2003; Parsons et al. 2003; Veith et al. 2004; Rivers et al. 2005, 2006) that is well known to the bats as a hibernaculum. Several lines of evidence suggest that the primary function of swarming is mating. This is supported by the spatial and genetic structure of swarming populations, bat vocalizations, the reproductive status of swarming males, and observations of copulations during autumn swarming (Moffat 1922; Furmankiewicz and Altringham 2007; Furmankiewicz 2008; Furmankiewicz et al. 2013). Therefore, swarming has a primary mating function and swarming sites play a role as hot spots for gene flow (Kerth et al. 2003; Furmankiewicz and Altringham 2007; Bogdanowicz et al. 2012).

However, some copulations can also take place in colony roosts. This is supported by direct observations (Stebbings 1966; Horáček 1975; J. Furmankiewicz, unpublished), the genetic differentiation of colonies (Furmankiewicz and Altringham 2007), and the presence of adult males in colony roosts, both resident males and males visiting the colony only around the mating period in the autumn months. Some behaviors, such as an increase in the number of tandem flights and vocalizations in maternity colonies around mating time in August and September (Zieliński 2013; Przepiórka 2016), may also suggest that copulations take place in colony roosts. Chases in different bat species have been observed in underground swarming sites (Thomas et al. 1979; Gottfried 2009; Maryjowski 2009; Furmankiewicz et al. 2013) and in the little brown bat *Myotis lucifugus* usually led to copulations (Thomas et al. 1979). However, the relative proportion of copulations at each site (colony roost vs. swarming site) and at each time of year and the mating success of swarming and colony males is not known. Nevertheless, it seems that the proportion of copulations in the colony is small. The colony males are relatives of some of the females, due to natal philopatry (this study), and they do not sire most of the colony offspring (Burland et al. 1999).

Underground hibernacula are distinctive sites known to bats because they hibernate there every winter, so bats can meet and swarm there. However, there are regions with no or a low number or quality of underground sites. In this case, the role of a meeting spot may be played by a selected area in the forest, which is suggested by bat behavior in city parks in spring. Bats were observed to vocalize in a similar way as in underground swarming sites at these sites, performing songflight displays only in selected spots of the parks every spring, and were never observed in other parts of the parks. This indicates that some afforested areas can also be used by bats as swarming sites in the same way as underground swarming sites. Such sites may be established in areas without underground hibernacula. It is likely that such spots were primary in such areas, as most underground mines are several dozen or several hundred years old. However, this requires more detailed analysis.

The mating season in *P. auritus* extends from autumn until spring, with 2 periods of active mating behavior, indicated by vocalizations, flight displays, and the reproductive state of males during the autumn and spring swarming. This is unusual among European bat species, including the swarming ones. Swarming in underground sites occurs only in late summer and autumn in other species (e.g., Fenton 1969; Bauerová and Zima 1988; Hanzal and Průcha 1996; Furmankiewicz and Górniak 2002; Parsons et al. 2003; Piksa 2008). Spring movements by this species in hibernacula are typically considered to just be emergence from the hibernacula and dispersal (e.g., Bauerová and Zima 1988; Degn et al. 1995; Hanzal and Průcha 1996; Jurczyszyn and Bajaczyk 2001). *P. auritus* leaves hibernacula in March, 1–2 months earlier than *Myotis* sp. (Daan 1973; Furmankiewicz and Górniak 2002). Therefore, it starts its activity earlier and moves to colony roosts. Shorter hibernation is probably caused by a preference by this species for low temperatures in hibernacula (Gaisler 1970; Bogdanowicz 1983) and a foraging strategy. The important components of its diet are moths (Lepidoptera), which can obtain from the surface (Swift 1998; Andreas et al. 2012) in early spring. Moreover, ovulation in *P. auritus*, as well as in other temperate-zone bat species, occurs in late April or May (Swift 1998; Racey and Entwistle 2000). This is supported by the proportion of inseminated *P. auritus* females found in hibernacula (Strelkov 1962). This proportion is low in autumn and increases to 50–81 % in March, with the remaining females being inseminated by the end of April (Strelkov 1962). Therefore, *P. auritus* may have two additional spring months for recovery and refueling after hibernation and for copulation, unlike the swarming *Myotis* species.

The vocal activity of swarming *P. auritus* is distinctive and unusual compared to other European temperate zone swarming species (Furmankiewicz 2004b; Furmankiewicz et al. 2013). A strong male-biased sex ratio in spring may explain the intense bat vocalizations, both in terms of the high number and greater diversity of the social calls. Vocal activity was lower in autumn, probably due to a higher number of females visiting swarming sites and a lower male-biased sex ratio. The low number of females present at swarming sites in spring increases competition among swarming males. Therefore, we assumed that females are attracted to the vocalizing males during the spring swarming period, which is the last chance for males to mate during the mating season (Furmankiewicz et al. 2013).

Males can advertise for mates using flight and vocal displays. Associations of bats in pairs and sometimes in triads have been observed in swarming *M. lucifugus* at swarming sites. Usually, males follow females and this interaction ends up with copulations (Thomas et al. 1979). Therefore, the vocalizations of bats flying and perching at swarming sites may announce their position to other bats and attract them. This will prompt the formation of bat associations followed by copulations. The attraction of bats to single played back social calls at our swarming sites confirmed this assumption. Furthermore, many individuals at one site may stimulate social behavior (i.e. through songflight displays) and increase the choice of mates, similar to the aggregation effect at lek aggregations and aggregations of territorial males in *P. nathusii* (McCracken and Wilkinson 2000; Jahelková and Horáček 2011). Moreover, vocalizations from swarming individuals may facilitate the recognition of relatives and colony members, as it is likely that they will visit the swarming site at the same time. Therefore, acoustic cues may be used to avoid mating with relatives, as it has been shown that some bat species produce vocally distinctive contact calls (Carter et al. 2012) and that bats can recognize each other based solely on these calls (Yovel et al. 2009; Voigt-Heucke et al. 2010).

The social vocalizations of *P. auritus* are lower and less diversified in autumn than in spring. The level of vocal activity and the vocal repertoire of other bat species that swarm at subterranean sites in autumn are also small (Barclay et al. 1979; Furmankiewicz and Górniak 2002; Rivers 2005; Gottfried 2009; Maryjowski 2009). Barclay et al. (1979) and Rivers (2005) argued that the proportion of social calls during swarming appears to be low because of the few social interactions of low complexity and the promiscuous mating system, which involves little selection. This appears to be common in swarming bats. No territorial and aggressive behavior or attempts by males to prevent access to females have been observed either at the swarming sites (this study) or in colony roosts with a high number of non-territorial males (Stebbings 1966, 1970; Howard 1995; Park et al. 1998; Entwistle et al. 2000; Duma et al. 2004). Bats visiting swarming sites remain there from a few hours to 2 nights, which makes it less favorable for them to monopolize a selected territory (Furmankiewicz 2008). It might also be impossible to defend females due to the huge number of competitors, the males would have to contend with; therefore, it is more favorable to attempt to mate with as many females as possible and then move on. Males *P. auritus* show no skew in their mating success (Burland et al. 2001); however, nonrandom mating has been observed in swarms of *M. lucifugus* (Watt and Fenton 1995) and in whiskered bats, *Myotis mystacinus*, *M. alcathoe*, and *M. brandtii* (Bogdanowicz et al. 2012). This suggests that females chose from among the swarming males.

The visitation frequency of *P. auritus* to swarming sites may also suggest a promiscuous mating system in this species. Bats revisit swarming sites within one season and they meet different conspecifics during each visit; therefore, both males and females might mate with different individuals. A promiscuous mating system may be a consequence of the presence of resident males in colonies, the philopatry of both sexes to maternity roosts, and the long-term occupancy of roosts by maternity colonies (i.e. throughout the whole non-hibernation season). Females may mate promiscuously to limit inbreeding among colony members and males to increase their reproductive success. Therefore, the lack of transitional defendable mating groups and roosts, as seen in some polygenic bat species (Altringham 2011), may also lead to promiscuous mating behavior.

Social behavior also appeared not to be simple in the maternity colonies of *P. auritus*; however, the vocal repertoire of the colony members was small. The bats emitted single social calls in tandem flights when emerging from and returning to maternity roosts and during dawn swarming. However, the calls were arranged in a sequence of several calls, and Murphy (2012) detected subcategories within those call. Bats responded to the social calls played back around colony roosts; therefore, calling by *P. auritus* in maternity roosts may be used to maintain contact among roost-mates, and so the social calls could function as contact calls. Members of the colony may also use visual, olfactory, and tactile signals to stay in contact with other colony members and their social behavior seems to be diversified. Tandem flights may function as visual signals and a means of scent propagation. Bats were also occasionally observed to keep face contact and to force the other bat to change positions (J. Furmankiewicz, unpublished). They were also seen to form subgroups within the roosts, with body contact between the members of each group; however, it was not possible to assess the composition and stability of these groups. Emerging and returning tandems seemed to be random, with no stable composition. It is also not known if all tandem flights in the colony roost involved associations of bats which came together or which were formed in the attic after calling and attracting one another. So calling behavior may show social bonds between colony members and encourage them to join what may lead to the formation of individual roosting associations. Therefore, social calls in colony roosts, along with tandem flights, may function as a greeting behavior among bats arriving at the roost after foraging. *P. auritus* forms stable philopatric colonies (Burland et al. 2006; Furmankiewicz, submitted) and every night colony members reunite after foraging or after resting in separate roosts. Greeting ceremonies are observed in some animals (e.g. many primate species, some canids, elephants, horses, dolphins, and parrots) during the fusions of social groups and involve recognition, approaches, and expressions of mutual affiliation, reassurance, and assessment (Bradbury and Vehrencamp 2011). *P. auritus* may display affiliative social bonds between colony members by emitting social calls and tandem flights during emergence from and returning to the roost. The emission of social calls in response to played back echolocation calls may also support this assumption. Moreover, we have never heard commuting or foraging bats emitting social calls; therefore, it is likely that bats use those calls only in or around the maternity roosts. Individuals arriving at colony roosts or after hearing the echolocation calls of conspecifics may call with social calls and await a response from the sender as a greeting behavior and reaffirmation of the sender's identity.

Complex social behavior (vocalizations, tandem flights, and emerging from and returning to roosts in groups), high stability, and philopatry to colony roosts and swarming sites suggest that both females and males of *P. auritus* form stable society-like groups. The potential causes of sociality in bats involve ecological constrains (e.g. roost limitations), longevity, social thermoregulation, predator avoidance, and cooperation with colony members (Kerth 2008). All of those factors may be mutually relevant in *P. auritus*; however, complex social interactions and group stability should be exclusively distinctive for cooperation with colony members (Kerth 2008). Understanding the reasons for leaving with cooperative partners is open for future research.

Conservation implications

Bats are very faithful to their summer roosts and swarming sites; therefore, their destruction or any changes that inhibit their use by bats may lead to a decline of a bat population. Most of the known roosts occupied by maternity colonies of *P. auritus* are warm and located close to forests (Entwistle et al. 1997; Duma et al. 2004). They are also often in large attics in big buildings, such as churches, palaces, and big houses. We noted that small attics or attics without large entrances (e.g. opened windows) were less likely to be inhabited by a maternity colony of

P. auritus, but there is anecdotal data. However, this confirms previous studies that bats require a specific roost type. The refurbishment of many buildings in recent years may lead to roost destruction or a decrease in roost quality, and hence it could cause the population decline and the destabilization of bat society. This point to the need for education and a stronger regime for the owners' of buildings with bat roosts, as legislation in Poland does not meet the standards required.

Swarming sites also need special care and protection, as they support large populations from large geographical areas and maintain gene flow between spatially isolated colonies (Parsons and Jones 2003; Rivers et al. 2006; Furmankiewicz and Altringham 2007). Swarming sites are often large underground hibernacula. Therefore, the use of gates to protect winter bat colonies should take into consideration their effect on swarming behavior, as the wrong shape of gate may hinder bats from using the underground site or make it more difficult (Pugh and Altringham 2005; Spanjer and Fenton 2005; Ławrynowicz 2011).

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Chapter 3
Sex-Biased Dispersal and Social Systems of Neotropical Emballonurids

Martina Nagy and Mirjam Knörnschild

Abstract The most common pattern of sex-biased dispersal in mammals including temperate bats is that females remain philopatric and males disperse from their natal groups. In contrast, sex-biased dispersal patterns in tropical bat species appear much more variable, ranging from all-offspring dispersal to female-biased dispersal and male-biased dispersal. The identity of the philopatric sex is essential for the kin structure of social groups (i.e. matrilineal relatives in species with female philopatry and patrilineal relatives in species with male philopatry) and thus for the evolution of social behavior. This book chapter contrasts sex-biased dispersal and the social systems of three well-studied Neotropical bat species of the family Emballonuridae. Two of these Neotropical Emballonurids exhibit exceptional female-biased dispersal and male philopatry in combination with resource-defense polygyny (greater sac-winged bat *Saccopteryx bilineata*) or female-defense polygyny (proboscis bat *Rhynchonycteris naso*). However, in the gray sac-winged bat (*Balantiopteryx plicata*) females are the more philopatric sex and the social system involves some sort of sexual segregation with mating probably taking place at male mating aggregations. To conclude, we discuss the evolutionary pressures driving the observed dispersal patterns and how sexual selection in Neotropical Emballonurids with male philopatry might shape bat sociality.

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3.1 Sex-Biased Dispersal in Neotropical Bats

Studies from the past decade revealed an astonishing diversity in dispersal patterns among Neotropical bats. Although to date only a handful of Neotropical bat species have been studied with respect to their dispersal behavior, the reported dispersal patterns span the whole spectrum of possible sex-biased and unbiased dispersal patterns. The predominant mammalian dispersal pattern of male-biased dispersal (i.e. dispersal is more prevalent in males and females tend to be faithful to their place or area of birth, termed philopatry) has been detected in common vampire bats (*Desmodus rotundus* Wilkinson 1985) and in gray sac-winged bats (*Balantiopteryx plicata*, Nagy et al. 2014). Thus far, these are the only examples of Neotropical bats that possess a dispersal behavior similar to temperate bats and the majority of mammals (Moussy et al. 2012; Lawson-Handley and Perrin 2007). In contrast, the remainder of Neotropical bats to which information on dispersal are available, exhibit rather exceptional dispersal patterns. Female-biased dispersal (i.e. dispersal is more prevalent in females and males tend to be philopatric) has been reported from two Emballonurid bats (greater sac-winged bat, *Saccopteryx bilineata*, Nagy et al. 2007; proboscis bat, *Rhynchonycteris naso*, Nagy et al. 2013) and from two Phyllostomid bats (Seba's short-tailed bat, *Carollia perspicillata* Fleming 1988; Cosson 1994; greater spear-nosed bat, *Phyllostomus hastatus* McCracken and Bradbury 1981). Two other species of Neotropical bats show a dispersal behavior without sex-bias; in the white-throated round-eared bat (*Lophostoma silviculum*) all offspring disperse from their natal colonies (Dechmann et al. 2007) and in Spix's disc-winged bats (*Thyroptera tricolor*) offspring of both sexes are philopatric to their natal groups (Chaverri and Kunz 2011).

The diversity in sex-biased dispersal patterns of Neotropical bats is paralleled by a similarly astonishing diversity in mating and social systems (McCracken and Wikinson 2000; Zubaid et al. 2006). Mating systems are widely believed to decisively influence the extent and direction of sex-bias in dispersal and, in general, dispersal in the polygynous and promiscuous social systems of mammals is assumed to be mediated by males (e.g. Greenwood 1980; Dobson 1982; Clutton-Brock and Lukas 2011). Female dispersal and male philopatry in mammals is frequently correlated with a rather rare mammalian male mating strategy of resource defense (Greenwood 1980). The mating system has also been proposed to influence the length of male breeding tenures and their longevity, whereby it determines whether females face a risk of father-daughter inbreeding, the latter of which should prompt females to disperse (Clutton-Brock and Isvaran 2007; Clutton-Brock 2009; Clutton-Brock and Lukas 2011). The unusual dispersal patterns in Neotropical Emballonurids provide us with the unique opportunity to test the validity of existing hypotheses on sex-biased dispersal and to gain new insights into the evolution of this important life history trait. In the remainder of this book chapter, we want to summarize what is known on the social systems and dispersal patterns of three well-studied Neotropical Emballonurids and on the evolutionary pressures that shape these patterns.

3.2 Female-Biased Dispersal in the Greater Sac-Winged Bat (*Saccopteryx bilineata*)

3.2.1 Social Organization and Mating System

Saccopteryx bilineata is a common inhabitant of lowlands between Southern Mexico and Southern Brazil. These bats use a number of different day roosts, all of which are generally well-lit. Day roosts (also referred to as colonies) include buttresses of large forest trees and cavities inside hollow trees, well-lit areas of caves, but also the inside or outside of abandoned and sometimes even inhabited human edifices (the most bizarre day roost we have ever witnessed was a group of about 30 *S. bilineata* roosting behind a fridge in a bar). Bats maintain a minimum distance of 5–8 cm to each other in the day roost. The basic social unit of *S. bilineata* is a one-male multifemale group that has been termed a 'harem'. Year-round, males defend a harem territory (i.e. 1–2 m^2 of vertical surface in the day roost) that includes the roosting sites of up to 8 females and 2–3 females on average. Thus, *S. bilineata* has a socially polygynous mating system and males follow a resource-defense mating strategy to get access to females. A colony may contain only one harem, but large colonies can have up to 12 adjacent harems and up to 60 adult individuals (Bradbury and Emmons 1974; Voigt et al. 2008). Particularly, larger colonies also contain a varying number of nonharem males. Nonharem males roost outside of harem territories in the same colony or sometimes may even defend a territory of their own. However, territorial nonharem males only occasionally have females roosting in their territories (Bradbury and Emmons 1974; Bradbury and Vehrencamp 1976; Voigt et al. 2008). *Saccopteryx bilineata* males typically gain harem access by queueing. Voigt and Streich (2003) performed a removal experiment, temporality taking out harem holders of their territories to observe which of the nonharem males took over the vacant territory. Usurpers belonged to small groups of nonharem males that spent their daytime close to the respective harems. Moreover, these so-called peripheral groups appeared to have a hierarchical structure according to their tenure in the colony. Thus, the nonharem males with the longest tenure in a peripheral group will be the first in filling an arising harem vacancy (Voigt and Streich 2003).

3.2.2 Female Dispersal

Female *S. bilineata* disperse from their natal colonies and immigrate into other colonies before they start reproducing; thus, female residents of a colony are unrelated immigrants (i.e. habitual female dispersal sensu Clutton-Brock and Lukas 2011). During a study period of 5 years (1996–2001) none of 71 juvenile females were observed to reproduce in their natal colony and 68 juvenile females (96 %) had already left their colony at an age of 6 months. The same study reported 37 female immigrants, none of which descended from members of the respective study colony (Nagy et al. 2007). Female dispersal in *S. bilineata* is very likely a strategy to avoid father-daughter inbreeding. In plural breeding mammals where several breeding females live in groups defended by one or more males, habitual female dispersal has been found to be consistently associated with male breeding tenures that exceed the females' ages at first conception. Therefore, if females were philopatric, they would risk inbreeding with theirs fathers, because the reproductive tenures of males will often not have ended before their daughters' onset of reproduction (Clutton-Brock 1989; Clutton-Brock and Lukas 2011). Age at first conception is about 7 months in *S. bilineata,* and females start reproducing the first mating season following their birth (Nagy et al. 2007). Mean tenure as a harem male based on data from 8 colonies was 1.9 ± 2.0 years. Harem males in the smallest colonies with only one harem male and without permanent nonharem males had the shortest tenures with on average less than one year (range 0.6–1.2 years). Harem males in the largest colony under study that contained 9–12 harems and 7–12 nonharem males were able to hold their harems for on average 2.9 years and up to 9.2 years (Nagy et al. 2012). Thus, the age at females' first conception in *S. bilineata* falls below the tenure duration of harem males, suggesting that female dispersal is an inbreeding avoidance strategy.

3.2.3 Male Philopatry

Roughly, half of the juvenile males born in a colony are still present in their natal colonies, the mating season following their births (63 % in a Panamanian population and 45 % in a Costa Rican population, Tannenbaum 1975; Nagy et al. 2007). Almost all males that become new residents of a colony are natal and thus, philopatric males (27 of 29 males, Nagy et al. 2007). This is also reflected in the typically philopatric origin of males that gain a harem position. A long-term study on eight Costa Rican *S. bilineata* colonies found that 45 of 62 males that took over a harem were philopatric individuals that descended from females and males of their respective natal colonies (Nagy et al. 2012). Apparently, harem take-over by immigrant males is more frequent in colonies that occasionally do not harbor any nonharem males (55 % immigrant harem males) as compared to colonies with permanent nonharem males (12.5 % immigrant harem males, Nagy et al. 2012). As a consequence of male philopatry and high levels of intracolony paternity, colonies of *S. bilineata* have a patrilineal social organization (Heckel and von Helversen 2003; Nagy et al. 2007; Fig. 3.1). Typically, several closely related males (fathers with their sons and grandsons as well as brothers) will roost simultaneously in a colony and compete over access to harem territories and females. For example, up to 70 % of pups resulted from females mating with someone other than their own harem male (Heckel and von Helversen 2003; Nagy et al. 2007). For many of these males local mate competition must therefore be severe, raising the question of how *S. bilineata* cope with the costs related to local mate competition. The solution to this problem

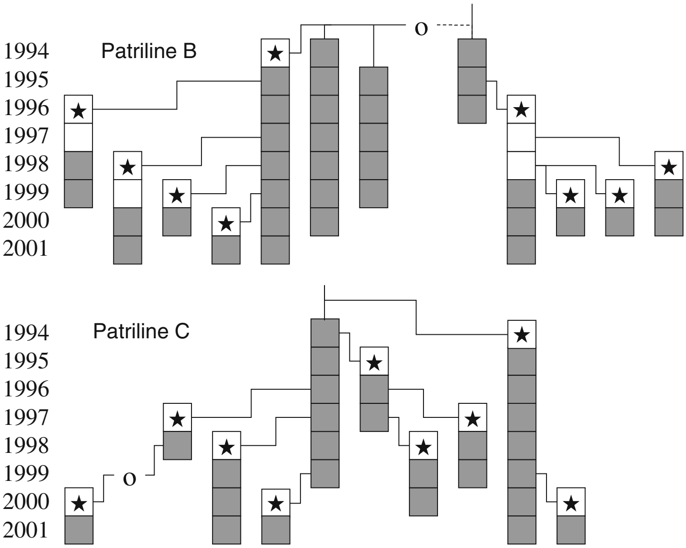

Fig. 3.1 Two of 12 patrilines of *Saccopteryx bilineata* from a large colony in Costa Rica that contained up to twelve adjacent harems. Patrilines were reconstructed based on paternity and kinship analysis. Each column depicts an individual male and each cell of the column a year for which paternities were determined (from 1996 until 2001) or reconstructed (before 1996). *Symbols*: *star* year of birth; *gray cells* years of presence in the colony; *white squares* years of presence outside the colony; *open circle* male from outside the colony; *solid line* relatedness of 0.5; *dashed line* relatedness of 0.25 (modified after Nagy et al. 2007). Patrilineal male kin, like grandfathers, fathers, sons, brothers, and cousins may roost simultaneously in a colony, competing over access to harem territories and females. Figure reproduced from Voigt et al. (2008), by courtesy of Oxford University Press

lies in the direct fitness benefits that males gain when living in multimale colonies. The reproductive tenure of harem males proved to increase with the number of male residents in a colony, whereas the number of breeding seasons a male succeeded in defending his harem was an important factor explaining variance in male lifetime reproductive success (Nagy et al. 2012). Intriguingly, in mammals evidence that male group size positively affects the reproductive tenure of males comes only from species where males are known or suspected to cooperate in female or territory defense (e.g., lions *Panthera leo* Bygott et al. 1979; red-fronted lemurs *Eulemur fulvus rufus*, Port et al. 2010). At present, evidence that male *S. bilineata* might likewise cooperate in excluding nonnatal males from settlement is only tentative. Because *S. bilineata* males profit from living in multimale colonies in terms of lifetime reproductive success, they should preferably immigrate into larger colonies. Immigration rate was, however, larger in smaller colonies. This suggests that resident males actively prevent immigration of nonnatal males and may be more effective in larger colonies with several resident males (Nagy et al. 2012). Excluding nonnatal males from settlement increases the chances that the patriline is maintained in a colony over large periods and therefore, can also assure future indirect fitness benefits (Nagy et al. 2007, Nagy et al. 2012). However, immigration attempts of nonresident males and/or attempts of immigrant males to expel harem males from their territories have only been documented anecdotally yet; such events are rare and, thus, difficult to observe. Further evidence for an active role of males in preventing settlement of nonnatal males comes from a learned vocal group signature in isolation calls that has been shown to reliably associate individuals with their natal colony. Isolation calls are usually used in mother-pup communication, but adult males of *S. bilineata* use isolation calls to appease more dominant males. Consequently, isolation calls may function as a 'password' allowing resident males to discriminate between natal and nonnatal males, but playback experiments are needed to verify this supposition (Knörnschild et al. 2012).

3.3 Female-Biased Dispersal in the Proboscis Bat (*Rhynchonycteris naso*)

3.3.1 Social Organization and Mating System

Rhynchonycteris naso is the smallest Neotropical Emballonurid; it forages for insects over the surface of moving water and is widely distributed in the lowland rainforests ranging from the South of Mexico to the South of Brazil and East of the Andes to Peru and Columbia (Hall 1981; Bradbury and Vehrencamp 1976). Commonly used dayroosts include the exposed boles of trees, the sides of cliffs but also manmade structures (e.g. underneath the overhanging roofs of buildings), preferably in the immediate vicinity of waterways (Bradbury and Emmons 1974; Nagy et al. 2013). In the dayroost, bats keep an individual distance of approximately 2–4 cm to each other and are visually cryptic due to their woolly and mottled pelage and two pale wavy lines on their backs (Dalquest 1957; Bradbury and Vehrencamp 1976). Small groups with only three individuals have been reported, but large colonies can consist of up to 50 *R. naso* with males and females at about equal numbers (Bradbury and Emmons 1974; Bradbury and Vehrencamp 1976). Bradbury and Emmons (1974) reported quite high compositional variability of social groups in Trinidad (29–86 %). In contrast, a long-term study from Costa Rica found that social groups were highly stable over long periods and individuals to show high fidelity to their day roosts (89–100 % fidelity, N = 131 individually banded bats, Nagy et al. 2013).

The mating system of *R. naso* has been described as a female-defense polygyny (Bradbury and Vehrencamp 1977a). Bradbury and Vehrencamp (1976) reported that their study groups were never observed to be without at least one adult male. This most-constant male was also the one that frequently returned to the roost at night, whereas other male group members rarely did so (Bradbury and Vehrencamp 1976). Their observations led them to suggest that there is some sort of dominance structure between the males of a colony (Bradbury and Emmons 1974, Bradbury and Vehrencamp 1976). Behavioral observations during the postpartum estrus of female

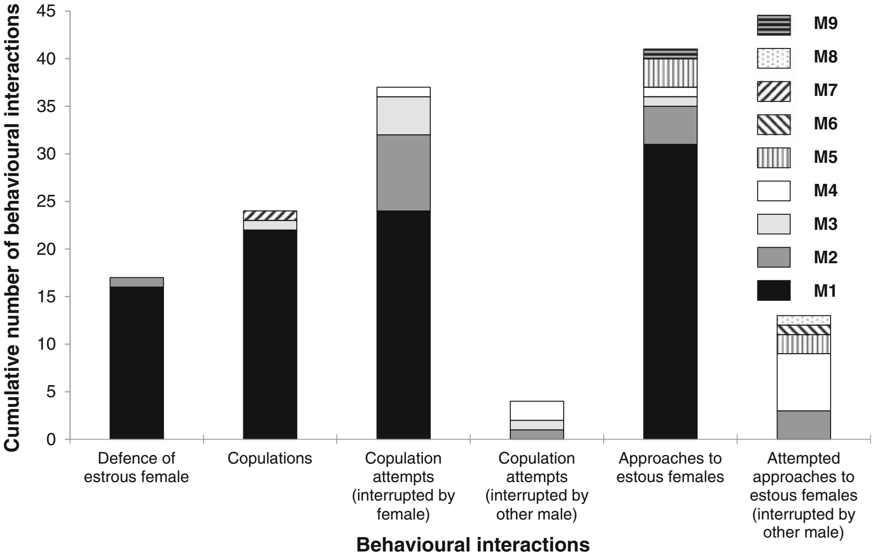

Fig. 3.2 Behavioral interactions (copulations, copulation attempts and defense of females) of *Rhynchonycteris naso* males with estrus females or competing males. Individual males (M1–M9) are represented by different colors or patterns. The majority of copulations, copulation attempts, and female defenses were performed by one most dominant male (M1). Figure reproduced from Nagy et al. (2013), by courtesy of John Wiley and Sons

R. naso in one Costa Rican colony showed that one of ten resident males performed the majority of copulations (92 %), copulation attempts (65 %), and defenses of estrus females (94 %, Nagy et al. 2013, Fig. 3.2). However, this apparently most dominant male sired just four of the 12 pups (33 %) fathered in the mating season preceding the observations. The remaining eight pups descended from five other males, four of which were also residents of the colony (Nagy et al. 2013). Admittedly, the surprisingly low fathering success of the by far most dominant male in the day roost might reflect differences in the males' dominance hierarchy of the preceding mating season, when the pups were sired. However, an alternative explanation could also be that direct defense of females in the day roost is not the only male mating strategy. There is preliminary, hitherto unpublished evidence from an ongoing PhD-thesis of Linus Günther on reproductive strategies of *R. naso* indicating that some sort of territorial defense might also be part of male mating strategies.

3.3.2 Female Dispersal

Just like in *S. bilineata,* all female offspring of *R. naso* leave their natal colonies before sexual maturity to disperse and immigrate into another social group. Evidence for female dispersal comes from the observation that 21 females banded as juveniles disappeared from their natal colonies within their first year of life. Furthermore, genetic paternity analysis on females captured and banded as subadults revealed that only 2 of 39 of them descended from adult members of their resident colonies (Nagy et al. 2013).

Females typically give birth the year following their own birth and first conception is rather early in life, at an age of about 10 months (Nagy et al. 2013). The median minimum tenure of males (1.65 years) was found to exceed the age of females at first conception. The actual tenure of males surely exceeds the minimal tenure estimate, because many bats were captured as adults or were still present in the social groups at the end of the study (Nagy et al. 2013). Natal dispersal of females in *R. naso*, therefore, has probably evolved to avoid father-daughter inbreeding (Clutton-Brock 1989; Clutton-Brock and Lukas 2011).

3.3.3 Male Philopatry

Evidence that males are faithful to their natal colonies in *R. naso* is provided by both observational and genetic evidence. Ten of 22 male pups (46 %) were still roosting in their natal colonies at an age of one year and a substantial proportion of males captured as subadults roosted together with one or both parents in the same colony (71 %, Nagy et al. 2013). Notwithstanding the high rate of male philopatry, immigration of males into established colonies is apparently not uncommon in *R. naso*. Several males transferred back and forth and were residents of two colonies or relocated permanently to another colony. In addition, philopatric and immigrant males were identified as sires of colony offspring (Nagy et al. 2013). So far data on the frequency of male immigration, degree of relatedness of males in colonies (i.e. patrilines) and success of males' reproductive strategies is lacking for *R. naso*.

3.4 Male-Biased Dispersal in the Gray Sac-Winged Bat (*Balantiopteryx plicata*)

3.4.1 Social Organization and Mating System

Balantiopteryx plicata live mostly in arid to semiarid areas with pronounced seasonality and all sites studied in Guerrero (Mexico) and Guanacaste (Costa Rica) underwent strong seasonal changes in rainfall (Bradbury and Vehrencamp 1976; López-Forment 1979; Arroyo-Cabrales and Jones 1988). These bats are distributed from Western Mexico along the Pacific to Costa Rica (Arroyo-Cabrales and Jones 1988). Day roosts used by *B. plicata* include well-lit parts of caves, crevices, mines, cliffs, the underside of boulders and also buildings (Arroyo-Cabrales and Jones 1988, López-Forment 1979). Colonies can contain up to 2,000 individuals (25 bats on average) and are the largest social groups known among Neotropical Emballonurids (Bradbury and Vehrencamp 1976; López-Forment 1979). As is typical for many Emballonurids, individuals roost without body contact and maintain a distance of about 20 cm to one another in the day roost (López-Forment 1979).

Information on the social system of *B. plicata* is still rather scarce, and thus at this point conclusions on the social organization and mating system of this bat are often deduced from circumstantial evidence. Females and males have been reported to roost intermixed in their colonies, and no subdivision of the roosting area into territories was observed (Bradbury and Vehrencamp 1976). However, in our main study colony, located in the La Casona Museum in Santa Rosa National Park in Costa Rica, the few females (4–8) present tended to roost close to each other (MN and MK unpublished observation) and census data on banded individuals suggest that day roosts contain several social groups with constant membership of bats (Nagy et al. 2014). The same population of bats also returned to the La Casona Museum at night. Likewise, bats were highly faithful to their social groups at night, but surprisingly membership to social groups in the day roost was not in accordance with nightly social group membership. Bats roosting together in the night roost originated from different social groups of the day roost. At present, the significance of these changes in social group membership between day and night roost remains unknown (Nagy et al. 2014).

Social behavior within the day roost is dominated by unusually high levels of aggression between males as reflected in an almost fourfold higher percentage of aggressive events in *B. plicata* males (9.2 % of total time, Table 3.1) as compared to for example males of *S. bilineata* (2.5 % of total time per hour in the state ‘aggression’; MK unpublished data). Males spent significantly more time in aggressive interactions than females (Mann-Whitney U test: $U = 0$, $N1 = 10$, $N2 = 4$, exact $P = 0.002$, corrected $\alpha = 0.025$; Table 3.1) and displayed significantly more aggressive events than females (Mann-Whitney U test: $U = 0$, $N1 = 10$, $N2 = 4$, exact $P = 0.002$, corrected $\alpha = 0.05$; Table 3.1). During our observation, pups displayed no aggressive behavior at all (Table 3.1).

In polygynous *S. bilineata* and *Artibeus jamaicensis,* aggressive interactions among males are often associated with competition for preferred roosting space in the day roost (Voigt et al. 2008; Ortega et al. 2008). We investigated whether the same could be the case in *B. plicata* by monitoring all aggressive interactions on twelve successive days for 60 min after 30 min of habituation (ad libitum sampling sensu Altmann 1974). Aggressive interactions among males often forced the inferior bat to relocate in the day roost. Thus, we monitored the spatial position of the aggressor prior to displacements to test whether dominant bats were predominantly found in the center or periphery of bat groups or alone. The spatial position of the aggressor after displacements was monitored to investigate whether the displacement occurred in the context of competition for preferred roosting places. If this was the case, we expected the aggressor to occupy the spatial position of the displaced conspecific. The aggressor’s behavior was monitored to assess the most prevalent behavior causing displacements. In total, we monitored 494

Table 3.1 Time-budget data for different behavioral states and events exhibited by *B. plicata* in the day roost

Behavioral states	Males	Females	Pups
	States per hour [%]		
Resting	84.5	90.1	95.2
Aggression	9.2	1.1	0.0
Grooming	5.9	7.6	3.9
Rocking	0.4	0.5	0.2
Shaking and resistance	0.0	0.7	0.7
Behavioral events	Nr. of events per hour		
Crawling position change	1.7	1.7	0.3
Flying position change	2.2	0.6	0.2
Wing flick	1.5	1.3	0.1
Wing blow	2.2	0.3	0.0
Bite	0.8	0.1	0.0
Aerial chase	1.7	0.0	0.0
Collision	1.8	0.0	0.0
Yawn	0.4	0.2	0.1
Push-up	0.4	2.0	0.3
Teat switch	0.0	0.0	1.6

Mean values for ten males, four females and their volant, nursing pups are shown

Table 3.2 Count data on aggressive interactions of *B. plicata* bat dyads in the day roost resulting in displacements (720 min of total observation time)

Position of aggressor prior to displacement	Position of aggressor after displacement				
	Return to previous position	Remain at position of displaced bat	Move to new position	No movement	Sum
Center of bat group	72	64	82	30	248
Periphery of bat group	37	40	100	2	179
Alone	4	17	46	0	67
Sum	113	121	228	32	494

displacements in 720 min of observation (Table 3.2). Aggressors usually approached their opponents on the wing landing next to or directly on them, but displacements were also caused by bats crawling or stationary flicking their wings (flying: 329; crawling: 133; stationary: 32; Chi-Square test: $\chi2 = 276.98$, df = 2, $p < 0.0001$; corrected $\alpha = 0.0167$). Prior to displacements, the majority of aggressors were roosting in the center of a bat group, not at its periphery or alone (Chi-Square test: $\chi2 = 101.35$, df = 2, $p < 0.0001$; corrected $\alpha = 0.025$; Table 3.2). After displacements, aggressors moved to a new roosting position significantly more often than they remained at the position of the displaced opponent or returned to their previous position (Chi-Square test: $\chi 2 = 53.55$, df = 2, $p < 0.0001$; corrected $\alpha = 0.05$; Table 3.2). On rare occasions (6.5 % of cases), the aggressor displaced a conspecific without an accompanying position change; this happened mainly when the aggressor was roosting in the center of a bat group and displaced a fellow group member by flicking its wing (30 of 32 cases; Table 3.2). Thus, competition for preferred roosting places is an unlikely explanation for the unusually high level of male aggression in the day roost. In 2009, when the aggression observations took place, the La Casona colony contained 116 bats on average, six of which were females (Nagy et al. 2014). Therefore, it is also unlikely that the more than 100 resident males were competing for access to the few female residents. One possibility is that male aggression in the day roost serves to establish some sort of dominance that might become important in the mating season. For *B. plicata* it has been suggested that mating occurs at male mating aggregations, which are traditional or species specific sites that are visited by females only for mating (Bradbury and Vehrencamp 1977a, see also next paragraph).

Many colonies of *B. plicata* have highly male-biased sex-ratios and the proportion of males in a colony has been found to range from 30–100 % (López-Forment 1979; Bradbury and Vehrencamp 1976; Nagy et al. 2014). The sex-ratio in a colony did not change from the parturition period (July and August) to the mating period (January and February) and also remained unchanged over several years, suggesting that in some *B. plicata* colonies males constantly prevail (Nagy et al. 2014). It has been suggested that the male-bias in colonies is caused by high female mortality leading to a male-biased population sex-ratio (Lòpez-Forment 1979). However, recent evidence shows that male and female tenure as well as survival from one year to the next are comparatively similar among the sexes (Nagy et al. 2014) and, in fact, López-Forment (1979) also caught almost equal numbers of males and females during his study. Thus, a population sex-ratio biased towards males appears improbable. Instead, a more plausible explanation could be that highly male-biased colonies represent year-round male mating aggregations that are visited by females during the mating season (potentially lek arenas; Bradbury and Vehrencamp 1977a; Nagy et al. 2014). Male calling activity has been noted to be increased and well audible from a distance in large colonies during the copulation period (Bradbury and Vehrencamp 1977a, MN and MK unpublished data) and might serve for attracting females to male mating aggregations during the mating season.

3.4.2 Female Philopatry

Genetic and behavioral data provide evidence of female philopatry in *B. plicata*. A fragment of the mitochondrial d-loop region was sequenced for bats of three day roosts, revealing that all females of a given day roost shared the same haplotype (Fig. 3.3). The same study reported that two of four female pups were observed to roost in their natal colony as adults, and that one of these females gave birth to a

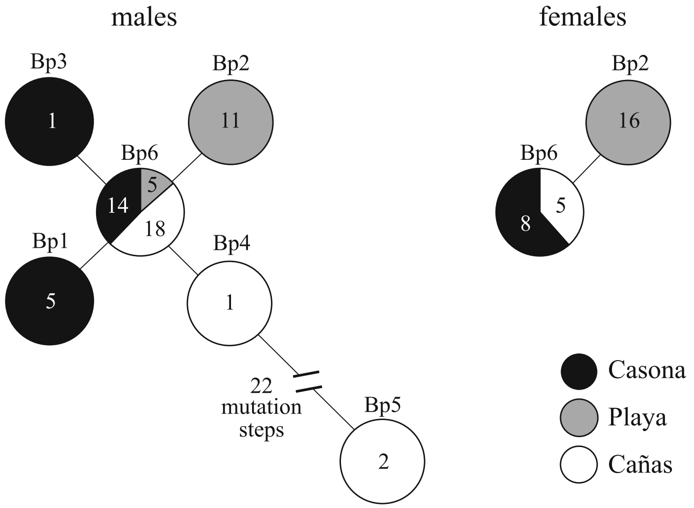

Fig. 3.3 Haplotype network of *Balantiopteryx plicata* males and females based on a 239 bp fragment of the mitochondrial d-loop region and on data from three day roosts (Casona, Playa and Canas) from Costa Rica. Circles depict individual haplotypes and numbers inside of circles indicate how often a haplotype was detected per day roost. Genetic variation within a day roost was always higher in males than in females, suggesting that gene flow is mediated by males. Figure reproduced from Nagy et al. (2014), by courtesy of Springer

pup in its colony of birth (Nagy et al. 2014). In contrast, and based on considerably larger sample sizes of banded female pups, reproduction of females in their natal colonies has never been witnessed in *S. bilineata* nor in *R. naso* (Nagy et al. 2007; Nagy et al. 2013).

Philopatry is usually considered the optimal strategy for female mammals (Clutton-Brock and Lukas 2011). Dispersing females frequently incur substantial fitness costs because of lower feeding efficiency (Young and Monfort 2009) and because the energetic costs of dispersal may delay breeding and reduce reproductive potential (Ronce 2007; Fisher et al. 2009). Furthermore, philopatric females can profit from improved fecundity and breeding success when associating with kin (e.g. Kawata 1990; König 1994). Bradbury and Vehrencamp (1977b) compared costs of parental investment among female *B. plicata*, *R. naso*, *S. leptura,* and *S. bilineata* and found *B. plicata* to incur the highest parental costs. Among the studied Neotropical Emballonurids, *B. plicata* experiences the highest seasonality in food supplies with a marked minimum during the dry season that coincides with females' gestation and the lowest adult survival rates (López-Forment 1979, Bradbury and Vehrencamp 1976). In Guanacaste, Costa Rica, males of this species had a 23 % lower body weight during the dry season as compared to the rainy season (Bradbury and Vehrencamp 1976). Therefore, environmental constraints might have favored female *B. plicata* to remain philopatric. By settling in the natal group, females can profit from knowledge of and access to nearby foraging grounds.

Tenure of males exceeds the age of females at first conception (average 1.56 versus 0.5 years, respectively, Nagy et al. 2014). Thus, it appears that female *B. plicata* are philopatric despite the risk of father-daughter inbreeding. However, possibly female philopatry does not create an inbreeding risk in *B. plicata*. This would be the case if further studies can corroborate that male-biased colonies function as male mating aggregations that are visited by females for mating. Then philopatric females would not roost with their fathers in the same colonies, and female philopatry would not cause an inbreeding risk.

3.4.3 Male Dispersal and Philopatry

Genetic and behavioral data suggest that the males of a given day roost constitute both philopatric and immigrant individuals. The analysis of the mitochondrial d-loop revealed higher diversity indices in males than in females and lower genetic structure between the males of various day roosts than between the females of various day roosts. This suggests that gene flow is higher among males and that males thus mediate dispersal (Nagy et al. 2014). However, the most frequent haplotype among males of a colony was in all colonies identical to the single haplotype females of a colony shared (Fig. 3.3), indicating that some males might descend from colony females and might therefore be philopatric. In accordance with genetic data, all four males banded as pups settled in their natal colony (Nagy et al. 2014). However, immigration of males could not be observed because of incomplete banding of bats (Nagy et al. 2014).

3.5 Conclusion

Female age at first conception falls below the breeding tenures of males in all three Neotropical Emballonurids contrasted in this book chapter, but only in *S. bilineata* and *R. naso* females disperse in accordance with a father-daughter inbreeding strategy (Nagy et al. 2007, 2013). We believe that female philopatry in *B. plicata* is probably favored by environmental constrains, because of a marked insect shortage during gestation in the arid and semiarid areas inhabited by this species (Bradbury and Vehrencamp 1976; 1977b; López-Forment 1979, Arroyo-Cabrales and Jones 1988). At present, male mating aggregations that females visit during the copulation period are the most likely mating system for *B. plicata* (Bradbury and Vehrencamp 1977a; Nagy et al. 2014). In such a scenario, philopatric females would not roost together with their fathers in a colony and no inbreeding risk would arise from female philopatry in *B. plicata*. In two other bat species (*Plecotus auritus* and *Thyroptera tricolor*), colonies contain philopatric individuals of both sexes and females have been demonstrated to mate with males from outside their own colonies (Burland et al. 2001; Buchalski et al. 2014). Thus, it appears that inbreeding avoidance plays an important role in shaping female dispersal and mating decisions in bats. Considering that longevity, year-round stable mixed-sex groups and the onset of female reproduction within the first year of life are traits shared among many Neotropical bats (Barclay and Harder 2003, McCracken and Wilkinson 2000), we predict that many Neotropical bats may in fact have dispersal patterns that deviate from typical mammalian male-biased dispersal.

Male philopatry seems to occur in *S. bilineata*, *R. naso,* and *B. plicata*, although in the latter species dispersal is more prevalent in males than in females (i.e. male-biased dispersal in *B. plicata*). This stands in contrast to the substantial differences in the mating systems and male mating strategies of these species. Whereas, *S. bilineata* males clearly follow a resource-defense mating strategy, with possible cooperation between related colony males (Nagy et al. 2012), it appears that direct female defense plays an important role in *R. naso* (Nagy et al. 2013) and that *B. plicata* probably form year-round male mating aggregations (possibly resembling lek arenas, Nagy et al. 2014). Thus, the common correlates of male philopatry in mammals (resource-defense by males and/or cooperation between males, Greenwood 1980, Lawson Handley and Perrin 2007) are apparently not sufficient to explain the prevalence of male philopatry in Neotropical Emballonurids. However, we must admit that to date for example, cooperation between related *R. naso* males has not yet been considered and that the mating system of *B. plicata* is poorly understood. Only long-term studies on banded bats that involve estimates of males' lifetime reproductive success with genetic tools will help us to understand which selective pressures are important in shaping male philopatry in these and other species.

Bats are exceptionally long-lived, social mammals and the majority of bats live in groups (McCracken and Wilkinson 2000, Kunz and Lumsden 2003). However, the reasons for bat sociality are still subject to much debate: proposed causes such as ecological constraints (e.g. roost limitation), physiological demands (e.g. thermoregulation), and demographic traits (e.g. longevity) do not seem to be able to fully explain why bats are social (Kerth 2008). Much of what we know about bat sociality is based in studies of female bats from the temperate zone (but see e.g. Dechmann et al. 2010) and thus typically focuses on naturally selected traits that enhance the fitness of females (but see Safi and Kerth 20s07, reviewed in Kerth 2008). In contrast, Neotropical bats often permanently live in polygynous/promiscuous mixed-sex groups and kin structures may often differ from temperate bats because of female dispersal and male philopatry (Bradbury and Vehrencamp 1977a, McCracken and Wilkinson 2000, Kunz and Lumsden 2003). This raises the question of how sexual selection in addition to natural selection may shape sociality of bats in the Neotropics.

One possible explanation for how sexual selection might shape bat sociality may constitute in the benefits of cooperating with other males in female defense. For example in *S. bilineata,* males gain direct and indirect fitness from roosting in multimale groups, and may even form cooperative alliances (Nagy et al. 2012). In *A. jamaicensis,* dominant males with large harems profit from the presence of related subordinates in their harems (Ortega et al. 2003). Female choice plays an important role in *S. bilineata* (Voigt et al. 2008) and although females can choose freely among the males in a colony, they generally mate with the males of their resident colony (Heckel and von Helversen 2003). Female *R. naso* probably also mate only with colony males (Nagy et al. 2013). If the males of a colony represent the pool of males available for mating, females should have a vital interest to immigrate into colonies that contain several males, thereby possibly selecting males to be more social. Due to frequent female philopatry maternal support is largely directed at daughters in mammals (e.g. in cercopithecine primates, Silk 2009) and support of sons is rare due to the general absence of male philopatry. In mammals, maternal support of sons has been documented from bonobos and chimpanzees, both of which have female-biased dispersal (Boesch 2009; Surbeck et al.2011). Female support of daughters is also known from bats (e.g. allogrooming between mother daughter pairs, Kerth et al. 2003), but female support of sons in male philopatric species of bats has not yet been considered. For example, *S. bilineata* mothers could gain substantial inclusive fitness by promoting their sons' establishment in the natal colony. Immigration of males into new colonies is rare and suitable roosts to establish new colonies are probably rare as well (Nagy et al. 2007, Nagy et al. 2012).

In conclusion, we propose that studying the diverse social systems and frequently exceptional sex-biased dispersal in Neotropical bats will contribute to our understanding of how evolution has shaped sex-biased dispersal patterns in mammals. Overall inbreeding avoidance seems well in accordance with female dispersal in Neotropical bats, but the factors driving male philopatry are less evident. There is a clear need for more longitudinal studies that incorporate genetics to study social systems and dispersal in Neotropical bats. In addition, a better understanding of social organization, mating systems, male mating strategies, and social interactions of Neotropical bats might grant us a better understanding on sexually and naturally selected causes of bat sociality.

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Chapter 4
Should I Stay or Should I Go? Fission–Fusion Dynamics in Bats

Krista J. Patriquin and John M. Ratcliffe

Abstract Animal species with fission–fusion dynamics are characterized by variable group size and composition, as individuals move freely among a social network. Patterns consistent with fission–fusion dynamics appear to be widespread in bats and interest in these patterns has advanced our general understanding of proximate and ultimate explanations for fission–fusion dynamics. Here, we explore the following questions: (1) Why do bats switch roosts? (2) Why do not group members move together? (3) Do bats form social bonds despite frequent roost switching? (4) If group members do form social relationships, what shapes these relationships? (5) How are social relationships maintained in these dynamic systems? (6) What does our understanding about fission–fusion in bats tell us about the evolution of fission–fusion dynamics in general? In our review, we show that bats switch roosts for a combination of reasons, including to reduce predation, parasites, and disease, and to minimize commutes. The strongest evidence, however, suggests bats switch roosts to seek more suitable roosts when roost quality changes. However, the degree to which each of these factors influences roost switching varies between individuals, across species, and depends on preferred roost type and roost availability. Group members may not move together because they experience different perceived costs and benefits of remaining in a group. Bats apparently use a combination of spatial and sensory information to relocate group members and maintain social bonds. Bat populations with fission–fusion dynamics likely benefit from social thermoregulation, and share information about roosts and foraging sites. Although our understanding of these dynamics has improved in recent years, many questions remain. For instance, a better understanding of the proximate factors driving fission–fusion dynamics is required. Establishing the levels at which bats sharing the same roost interact, together with network analyses, would also advance

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our understanding of relationships within these dynamic groups. Together, answers to these and other questions will help us to better manage bat populations and their habitat.

Social systems, defined by group size, stability, composition, and interactions among group members (Hinde 1976), vary along a continuum. At one end of this continuum are the eusocial insects and mammals. With the exception of rare dispersal events, group size and composition vary only with births and deaths of group members in eusocial species, as the costs of dispersal are high. Consequently, individuals interact regularly, which favors cooperation among familiar group members. At the same time, group members are typically very closely related, favoring nepotism, where individuals preferentially cooperate with relatives. Ultimately, these conditions have favored altruism, and most individuals forego their own reproductive efforts and instead care for the offspring of a few breeding group members (Choe and Crespi 1997; Burda et al. 2000; Bourke 2014).

At the other end of the continuum are fission–fusion societies, where larger groups periodically split into multiple smaller groups that later regroup, or, in other instances, individuals move freely among a network of multiple social groups (reviewed in Aureli et al. 2008). Despite the dynamic nature of these groups, individuals interact nonrandomly, with some group members spending more time together than with others. In some cases, group members who interact regularly are also related, but relatedness is often highly variable within groups. Group members have the opportunity to engage in social behaviors, such as cooperation and nepotism, and therefore these groups represent more than passive aggregations around common resources. Although fission–fusion dynamics are assumed to be relatively widespread, they have been difficult to quantify making them less well understood compared to more stable social systems (reviewed in Aureli et al. 2008).

Nevertheless, fission–fusion dynamics have been quantified for a variety of primates, cetaceans, and ungulates (Aureli et al. 2008), with most of our understanding coming from studies of a few well-documented species, including African elephants (*Loxodonta africana;* Wittemyer et al. 2005; Archie et al. 2006), bottlenose dolphins (*Tursiops truncatus*; Connor et al. 2000; Lusseau et al. 2006), and chimpanzees (*Pan troglodytes*; Lehmann and Boesch 2004). Evidence from these species supports theoretical predictions that fission–fusion dynamics, like other social systems, are influenced by life history, reproductive strategy, phylogeny, and resource stability (Clutton-Brock and Janson 2012). For instance, fission–fusion has evolved primarily in long-lived animals with high offspring investment, high female philopatry, and where individuals occupy environments that vary within their lifetimes (Aureli et al. 2008; Couzin and Laidre 2009). At the same time, because related and unrelated group members interact repeatedly, cooperative behaviors, such as social grooming, cooperative offspring care, cooperative feeding, and group defense, have evolved in these seemingly random systems (Aureli et al. 2008).

Bats are also long-lived animals with high offspring investment, and many species show high female natal philopatry and occupy moderately variable environments (Kunz and Fenton 2003). Studies over the past 15 years have demonstrated that several species also live in fission–fusion societies where group members cooperate (Kerth 2008a). Fission–fusion in bats generally refers to the group dynamics of individuals found roosting together during the day, where subgroups or individual group members switch among roosts, leading to changes in group size and composition. In the neotropics, for example, females typically live in relatively stable year-round harems with one or two resident males, but they also move periodically. For example, female short-nosed bats (*Cynopterus sphinx*) switch as infrequently as every 4 years (Storz et al. 2000), while Spix's disk-winged bats (*Thyroptera tricolor*) may switch roosts (harems) almost daily (Vonhof et al. 2004). In temperate regions group dynamics are highly seasonal and much more fluid. There, following hibernation, females form summer groups where they give birth and raise their offspring while males are typically solitary or live in small all-male groups. Throughout the summer, females switch roosts, but not as a cohesive group, resulting in variable group size over time. As a result, a colony consists of multiple social groups interconnected by the movement of group members between groups (Patriquin et al. 2010; Kerth and Van Schaik 2011).

While roost switching (or roost fidelity) is widely documented in bats (see Lewis 1995 and Barclay and Kurta 2007 for reviews), group size, stability, composition, and social relationships within groups have been quantified for only a few species, and most of our understanding comes from temperate vespertilionids (Table 4.1). Nevertheless, work with these species has revealed several trends, which we will draw on to answer the following questions: (1) Why do bats switch roosts? (2) Why do not group members switch roosts together? (3) Do bats form social bonds despite the fluid dynamics of fission–fusion? (4) If so, what shapes these bonds and how long do they last? (5) Is there evidence of cooperation and/or nepotism? From there, we will identify gaps in the current knowledge about fission–fusion in bats and offer suggestions for future directions. By examining fission–fusion in bats, we will then determine whether the factors shaping these systems are similar to those in other taxa, in turn providing further insight to the evolution of fission–fusion dynamics.

Fission–fusion dynamics in various taxa, including bats, has been discussed to varying degrees elsewhere (Couzin 2006; Aureli et al. 2008; Kerth 2008a; Couzin and Laidre 2009); our goal here is to synthesize and expand on previous discussions to provide a single, cogent review of our current knowledge with an aim to identify existing gaps and future directions. Our review will focus on sociality among females as much less is known about sociality in males (but see Safi 2008; August et al. 2014). Also, we will focus on dynamics in day roosts as little is known about group dynamics of bats in night roosts, with the exceptions of the false vampire bat (*Megaderma lyra*; Schmidt 2013) and the white-striped free-tailed bat (*Tadarida australis*; Rhodes 2007).

Table 4.1 Summary of fission-fusion dynamics in bats described to date*

Family	Species	Region	Roost type	Residency time (mean ± SD days)	Diet/foraging guild	Group composition
Vespertilionidae	*Myotis bechsteinii*; Bechstein's bat	Germany; temperate[a]	Primarily roost boxes, some tree cavities	N/A	Primarily gleaning insectivore	Adult females + young; matrilineal[14]; low average relatedness[15]; communities revealed by network analyses[16]
Vespertilionidae	*Myotis capaccinii*; long-fingered bat	Greece; warm temperate/subtropical	Caves and mines	Residency times N/A High fidelity with limited movement between seasons and some movement within seasons[23]	trawling	Primarily adult females + young[23]
Vespertilionidae	*Myotis daubentonii*; Daubenton's bat	UK; temperate	Roost boxes	N/A	Aerial insectivore over water?	Primarily adult females + young; male bachelor groups Network analyses reveal social groups within colonies[1]
Vespertilionidae	*Myotis nattereri*; Natterer's bat	UK; temperate	Roost boxes	N/A	Aerial insectivore	Primarily adult females + young with some males Network analyses reveal social groups within colonies[1]
Vespertilionidae	*Myotis septentrionalis*; northern myotis	North America; temperate	Tree cavities	Nova Scotia: 1.20 ± 0.49 to 1.26 ± 0.40[25,b] Kentucky: 2.4 ± 2.1 [29]	Gleaning and aerial insectivore	Females and young; network and cluster analyses reveal isolated colonies and interconnected subgroups within colonies[25]
Vespertilionidae	*Myotis sodalis*; Indiana bat	North America; temperate[a]	Exfoliating bark and tree cavities	3.3 ± 1.4; 4.0 ± 3.1[30]	Aerial insectivore	Adult females and young; network analyses suggest no obvious social groups within network[30]
Vespertilionidae	*Antrozous pallidus*; pallid bat	North America; temperate	Rock crevices	1.4 ± 0.7[18]	Gleaning insectivore	Adult females and young
Vespertilionidae	*Barbastrellus barbastrellus*; western babastrelle	Germany; temperate	Tree bark	2.0 ± 1.8[10]	Primarily aerial insectivore some gleaning	Adult females and young

(continued)

Table 4.1 (continued)

Family	Species	Region	Roost type	Residency time (mean ± SD days)	Diet/foraging guild	Group composition
Vespertilionidae	*Chalinolobus gouldii*; Gould's wattled bat	Australia; Warm temperate	Tree hollows and bat boxes	Boxes: 6.8 ± 1.4 Trees: 2.6 ± 0.9 [6]	Aerial insectivore	Males solitary; females solitary or in small groups NOTE: these were not maternity groups
Vespertilionidae	*Chalinolobus tuberculatus*; long-tailed bat	New Zealand; temperate	Tree cavities	1.7 ± 2.0 [20]	Aerial insectivore	Adult males + adult females and young
Vespertilionidae	*Corhynorinus rafinesquii*; Rafinesque's big-eared bat	North America; temperate[a]	Bridges, tree hollows, buildings	2.1 Maximum # days in a human-made roost: 4.9 ± 3.3 Tree roost: 3.2 ± 1.5[32] Primarily trees: 3.0 ± 0.4 (SE)[11]	Gleaning and aerial-hawking insectivore	Adult males, adult females and young; network analyses revealed distinct colonies and subgroups within one colony[11]
Vespertilionidae	*Eptesicus fuscus*; big brown bat	Canada; temperate	Tree cavities	1.7 ± 0.7 [34]	Aerial-hawking insectivore	Females + young
Vespertilionidae	*Nyctalus lasiopterus*; giant noctule	Spain; warm temperate/subtropical[a]	Tree cavities	2.68 ± 0.82[27]	Aerial insectivore and carnivore	Females and young; network and cluster analyses reveal distinct colonies and interconnected subgroups within colonies[27, 8]
Vespertilionidae	*Plecotus auritus*; brown long-eared bat	Germany; temperate[a,d]	Roost boxes	N/A	Gleaning insectivore	Adult females and young
Vespertilionidae	*Tadarida australis* white-striped free-tailed bat	Australia; warm temperate/subtropical[a]	Tree hollows	10.6 ± 7.9[28, a]	Aerial insectivore	Adult males + adult females and young
Thyropteridae	*Thyroptera tricolor*; Spix's disk-winged bat	Costa Rica; neotropics[a]	Furled leaves	N/A (assumed to be daily up to every 4 days based on leaf availability)	Primarily gleaning insectivore	Males + females + young Socially isolated colonies and interconnected communities (i.e., subgroups) revealed by cluster and network analyses [33, 3]

(continued)

Table 4.1 (continued)

Family	Species	Region	Roost type	Residency time (mean ± SD days)	Diet/foraging guild	Group composition
Pteropodidae	*Cynopterus sphinx*; greater short-nosed bat	India; paleotropics[a]	Tent (foliage)	N/A: bats occupy roosts up to 4 years; but females move among harems between years[31]	Frugivore	Harems: adult male + females and young Multiple harems can make up a single colony[31]

Family	Group size (mean # adults ± SD);	Association index/relatedness	Factors shaping bonds	Duration of relationships	Social behavior?
Vespertilionidae	Colony: 21–31[12,a] Roost group: 5.3 ± 0.3 to 6.1 ± 0.3[12,a] Social group: N/A	Fager's index (I_{ij}): 0.39 ± 0.03 to 0.50 ± 0.01[a, 12]; χ^2 index[12]: 81.9 ± 8.3 to 134.9 ± 9.0[a]	Reproductive condition[12] Maternal relatedness[12] Pairwise nuclear relatedness[16]	"Days to years" (precise values not estimated)[16]	Allogrooming[13]; naso–naso contact[13] xenophobia[15] information sharing[17] network analyses suggest information sharing within but not between colonies[16]
Vespertilionidae	Colony: N/A Roost group[g]: 1–125 adults, estimated from figures in [23] Social groups: N/A	Variable colony size within season suggestive of fission–fusion but associations not quantified[23]	N/A	N/A	N/A
Vespertilionidae	Colony: N/A Roost group[f]: 2–26[1] Social groups: N/A	Variable group size and network analyses suggestive of fission–fusion but no association indices[1]	Sex-biased[1]	SLAR: few (25 %) pairs together up to 100 days,; some within-sex pairs up to 400 or more days; between-sex pairs 100 to 300 days[1]	N/A
Vespertilionidae	Colony: N/A Roost group[f]: 2–35[1] Social groups: N/A	Variable group size and network analyses suggestive of fission–fusion but no association indices[1]	Sex-biased[1]	SLAR: roughly 50 % pairs together up to 100 days, with some bonds lasting more than 500 days -trends held for within-sex and between-sex pairs	N/A

(continued)

Table 4.1 (continued)

Family	Group size (mean # adults ± SD);	Association index/relatedness	Factors shaping bonds	Duration of relationships	Social behavior?
Vespertilionidae	*Nova Scotia*: Colony: at least 75 Roost group:19.6 ± 14.9[25] Social group: 2–24[25] *Kentucky*: Colony: 2–18[29] Roost group: N/A Social group: N/A	Half-weight index (HWI): 0.09 ± 0.16[25]	Reproductive condition[25] Age[25] Maternal relatedness[26] Pairwise nuclear relatedness[26]	SLAR: 10 to at least 75 days [25]	N/A
Vespertilionidae	Colony: N/A Max roost group: 109[30] Social groups: N/A	Roost use and network analyses suggest fission–fusion but associations not quantified[30]	N/A	N/A	Social foraging is possible[30]
Vespertilionidae	Colony: N/A Roost group: 1–90[18] Social group: N/A	Known pairs found together repeatedly, but associations not quantified[18]	N/A	N/A	Social transmission[2]
Vespertilionidae	Colony: N/A Roost group: 1–15 (including juveniles) Social group: N/A	Variable group size and movement of known individuals suggestive of fission–fusion but no association indices[10]	N/A	N/A	N/A
Vespertilionidae	Colony[f]: N/A Roost group[f]: 1–10[6] Social group: N/A	N/A [c]	N/A	N/A	N/A
Vespertilionidae	Colony[g]: 166–234[21] (including juveniles) Roost group[f]: 34.7 ± 23.4[20]	N/A pairs of bats recorded together more than expected from random binomial distribution of recapture rate[21]	N/A	N/A	N/A
Vespertilionidae	Colony: 75–125[32] Roost group: 18.3 ± 3.3 (SE) Social group: N/A	Changing group size and composition suggestive of fission–fusion but associations not quantified[32,, 11]	N/A	N/A	N/A

(continued)

Table 4.1 (continued)

Family	Group size (mean # adults ± SD);	Association index/relatedness	Factors shaping bonds	Duration of relationships	Social behavior?
Vespertilionidae	Roost group: 18.1 ± 12.1[34]	Pairwise sharing index (PSI): females from same matriline = 0.428 ± 0.208; from different matrilines = 0.360 ± 0.191[19]	Reproductive condition[34] Maternal & nuclear relatedness NS[19]	N/A	N/A
Vespertilionidae	3 colonies[e]: 61–114[a,27] Roost group: 14–60[27] Social group: N/A[27]	N/A	N/A	N/A	Network analyses suggest potential for information transfer within colonies but restricted between colonies[8]
Vespertilionidae	Colony: 9–17[a, 7] Roost group: N/A Social group: N/A	Fission–fusion implied by changing number of groups and size of groups, but associations not quantified[7]	N/A	N/A	N/A
Vespertilionidae	Colony: N/A Communal day roost group: 58–291[28, a]; satellite roost group: 1–21[28, a] Social group: N/A	Pairwise sharing index: -0.55 ± 0.18[28, a]	N/A	N/A	Vocalizations and swarming at night roost [28]
Thyropteridae	Colony: N/A Social group: 4.5 ± 2.18[33,a] Roost group: 3.3 ± 1.15[33, a]	Simple ratio: 0.66 ± 0.218[33]	Trend toward sex-biased bonds, but NS[33] Relatedness and reproductive condition not assessed	Standardized lagged association rate (SLAR): usually ≤ 100 days, up to almost 4 years[33]	Information sharing[4]

(continued)

Table 4.1 (continued)

Family	Group size (mean # adults ± SD);	Association index/relatedness	Factors shaping bonds	Duration of relationships	Social behavior?
Pteropodidae	Colony: 11.4 ± 6.7; 19.9 ± 11.3[31] Harems: 6.1 ± 3.5; 13.6 ± 8.5 [31]	Female movement between adjacent harems; known pairs found together across seasons but no association indices[31]	N/A	Known individuals found together across years [31]	N/A

*Based on a literature search in Web of Science using terms bat, fission, cryptic, population

NOTE Several studies have also investigated different network metrics—but the metrics used vary considerably, and therefore are difficult to summarize here

Colony = network of individuals interconnected by sharing roosts over time

Roost group = individuals physically located in the same roost together on the same day

Social group = individuals found roosting together more often than expected by chance over time

[a] Multiple colonies studied over multiple years; findings vary with year and colony

[b] See (9) for an earlier study in the same area

[c] Purpose of study was to examine role of ectoparasites on roost switching—noted that group size changed but did not quantify associations among group members[6]

[d] See 5 for description of mixed-sex groups in attics in the UK

[e] Originally referred to as social groups but later identified as analogous to colony

[f] Authors refer to groups as colony, but by our definition they were measuring roost groups

[g] Authors use social group and later subpopulation but there is limited movement between groups, so by our definition they are referring to colony

[h] Authors refer to a group within a cave as a colony, but later refer to evidence that all caves were visited by the same colony[22]

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4.1 Why Do Bats Switch Roosts?

Roost switching may be costly (Lewis 1995; Ellison et al. 2007); therefore it likely reflects an individual's attempt to balance the costs and benefits of group living (Lewis 1995; Kashima et al. 2013). For instance, bats appear to select roosts that offer protection from potential predators and that provide optimal conditions for thermoregulation (reviewed in Kunz and Lumsden 2003 and Barclay and Kurta 2007). At the same time, many species may live in groups, at least in part, to minimize thermoregulatory costs through group warming (Willis and Brigham 2007), but, as a result, may incur the costs of increased conspicuousness to predators and increased risk of transmission of diseases and parasites (Krebs and Davies 1995). Of course, living in social groups may also confer less tangible benefits, such as cooperation and nepotism (Carter and Wilkinson 2013a, b). As such, several explanations have been proposed for roost switching, none of which are necessarily mutually exclusive, including antipredation, reducing ectoparasite loads, reduced commuting distances between food and roosts, and change in roost quality (Barclay and Kurta 2007). We consider several plausible explanations in turn below.

4.1.1 Antipredation

As discussed in a recent review of the influence of predators on bat behavior, reduced predation risk is an often cited—but rarely tested—explanation for roost switching by bats (Lima and O'Keefe 2013). Certainly aerial and terrestrial predators attack bats emerging from roosts, and some predators have developed specialized hunting strategies for bats (Ancillotto et al. 2013; Mikula et al. 2013; Michaelsen et al. 2014; reviewed in Lima and O'Keefe 2013). Correspondingly, bats may select roosts, in part, to provide them protection from predators (reviewed in Kunz and Lumsden 2003 and Barclay and Kurta 2007), suggesting to some researchers that bats are likely "sensitive to day-to-day variation in the risk of predation" (Lima and O'Keefe 2013, p. 640). Moreover, a range of predators visit occupied roosts (simulated by placing fresh guano in roosts) more often than unoccupied roosts (Threlfall et al. 2013), supporting the idea that roost switching may be an effective antipredator strategy. Indeed bats leave roosts when directly attacked but there is little evidence that they respond to visual, acoustic, or olfactory cues of predators (Michaelsen et al. 2014; reviewed in Lima and O'Keefe 2013). Interestingly, Lima and O'Keefe (2013) argue that temperate bats are least likely to be influenced by predators, yet roost switching in bats is most common in these regions. Predation risk, by itself, does not appear sufficient to explain frequent roost switching.

The relative influence of predation risk on roost switching may vary between individuals and across species, and depends on roost type and the availability of alternative suitable roosts (reviewed in Lima and O'Keefe 2013). For several species, including little brown bats (*Myotis lucifugus*), pallid bats (*Antrozous pallidus*), Indiana bats (*M. sodalis*), and northern long-eared bats *(M. septentrionalis*), individuals may remain in a roost while other group members leave, and would therefore presumably still be at risk of predation (e.g., Barclay 1982; Lewis 1996; Carter and Feldhamer 2005; Patriquin et al. 2010), indicating that the relative costs and benefits of switching vary across individuals (reviewed in Barclay and Kurta 2007). Bats often show higher fidelity to man-made roosts, such as buildings and bat boxes (Lewis 1995; Kunz and Lumsden 2003; Evelyn et al. 2004; Lausen and Barclay 2006; Evans and Lumsden 2011), that are typically warmer and more stable and therefore result in higher offspring survival compared to natural roosts (Lausen and Barclay 2006). This despite some evidence suggesting predation risk is in fact higher at these structures (Michaelsen et al. 2014). Lausen and Barclay (2006), on the other hand, suggest bats in buildings are less vulnerable to terrestrial predators compared to bats in rock crevices, but these authors did not consider aerial predators. It appears, then, bats may trade-off predation risk in favor of optimal roost conditions (reviewed in Lima and O'Keefe 2013).

4.1.2 Minimize Commuting Distances Between Foraging and Roosting Sites

As Kunz and Lumsden (2003) point out, bats may switch roosts to be closer to feeding sites to minimize the costs of travel, yet there is little support for this hypothesis. Certainly, bats generally roost in areas closer to foraging habitat compared to randomly available roosts (Kingston 2013; Trevelin et al. 2013) and Lewis (1995) found several frugivorous species switch roosts to be closer to patches of fruit. Similarly, at least two insectivorous species, common pipistrelles (*Pipistrellus pipistrellus*) and soprano pipistrelles (*P. pygmaeus*), appear to switch to roosts that minimize commuting costs as distances between roosts and foraging sites are less than distances between consecutive roosts (Feyerabend and Simon 2000; Bartonička et al. 2008). However, when they moved to buildings during lactation, roosts were farther from their main foraging site (Bartonička et al. 2008), suggesting roost switching is not always driven by commuting costs. Indeed reviews of roost fidelity within roost areas have demonstrated that distances between roosts are typically less than distances between roosts and foraging sites, suggesting bats are not moving to be closer to foraging sites (Lewis 1995; Kunz and Lumsden 2003). In fact, distances traveled by common vampire bats (*Desmodus rotundus*) between roosts and foraging sites are often greater than between consecutive roosts (Wilkinson 1985) while no difference in distance between roosting and foraging sites was found for Hemprich's long-eared bats (*Otonycteris hemprichii*) roosting in rock crevices (Korine et al. 2013). Female Bechstein's bats (*Myotis bechsteinii*) found roosting together travel different distances to forage, with some traveling much farther than others (Kerth et al. 2001a, b), suggesting that in this species roost choice is not based on proximity to foraging sites, or at least not for all group members. Thus evidence that bats switch roosts to be closer to foraging sites is equivocal.

The relative importance of switching roosts to minimize commuting costs may vary with factors such as reproductive condition, roost type (and in turn availability), and diet. Soprano pipistrelles, among others, select roosts closer to foraging sites during lactation compared to postweaning (Bartonička et al. 2008), presumably because the costs of commuting during lactation are higher as females often return to roosts throughout the night to nurse their young (Kunz and Lumsden 2003). Some soprano pipistrelles move during lactation from bat boxes near their main foraging site during gestation to buildings farther away, which presumably offer different microclimates needed during lactation (Bartonička et al. 2008). Independent of reproductive condition or roost type, species like Hemprich's long-eared bats and Bechstein's bats may not benefit from attempting to roost closer to their prey that typically have unpredictable distributions, such as vertebrates or insects that do not swarm. Species like the Jamaican fruit-eating bat (*Artibeus jamaicensis*) may move closer to patchy, more predictable food, such as fruit or insect swarms (Barclay and Kurta 2007). Tent-making bats, which are capable of constructing roosts rather than relying on existing structures like trees, rocks, and buildings, could theoretically construct/switch roosts to be closer to foraging sites; this, however, has yet to be tested and evidence that bats are actually more likely to switch among relatively more permanent tents (Sagot and Stevens 2012) suggests tent-making and switching is not related to minimizing commuting distances. When examining factors that influence roost switching, and fission–fusion dynamics, it is important to consider species and population level differences in sex, reproductive condition, roost type, and diet.

4.1.3 Ectoparasites

Ectoparasites can impose significant costs to their hosts (Lourenço and Palmeirim 2007); as such, high parasite loads associated with a given roost may prompt bats to switch. A theoretical model demonstrates that bats may receive higher fitness benefits if they trade-off optimal roosts for lower ectoparasite loads (Kashima et al. 2013), which they can achieve by leaving roosts thus disrupting some parasites, particularly bat flies (Families Streblidae and Nycteribiidae), that must complete part of their life cycles on the roost substrate rather than on the host (Dick and Dittmar 2014). Empirical evidence suggests that the timing of roost switching by Bechstein's bats, common pipistrelles, and soprano pipistrelles, as examples, coincides with peak infestations and that switching reduces ectoparasite numbers by as much as half (Reckardt and Kerth 2006; Bartonička and Gaisler 2007; Bartonička and Růžičková 2013). Moreover, it has been reported that pallid bats and Gould's wattled bats (*Chalinolobus gouldii*) with higher ectoparasite loads switch roosts more often than those with lower parasite loads, suggesting bats leave roosts to escape high infestations (Lewis 1996; Evans and Lumsden 2011). Others argue that higher ectoparasite loads on Bechstein's bats that switch roosts less frequently is evident that roost switching is effective at reducing ectoparasites (e.g., Reckardt and Kerth 2007). Interestingly, Bechstein's bats appear to use information about prior roost occupancy to minimize their risk of reinfection (Reckardt and Kerth 2007). When provided a paired choice between new roost boxes and previously occupied, and thus potentially infested, roosts, Bechstein's bats preferred new roosts. Moreover, when given a choice between recently occupied roosts and roosts occupied in previous years, Bechstein's bats preferred older roosts that were less likely to be infested. Roost switching therefore appears to be an effective means for reducing parasite loads.

The relationship between roost switching and ectoparasite load is likely complicated by the kinds of ectoparasites involved. For instance, although bat flies move between bats via the roost substrate where they must complete part of their life cycle, mites move through direct contact between bats where they remain for their entire life cycle (Christe et al. 2000; Dick and Ditmar 2014). Also, unlike some mites, bat flies do not appear to elicit a grooming response (Godinho et al. 2013). It is therefore argued that roost switching is the only effective means for reducing the prevalence of bat flies but is unlikely to affect mites (e.g., ter Hofstede and Fenton 2005; Reckardt and Kerth 2007). However, roost microclimate affects both bat fly and mite survival (Bartonička and Gaisler 2007; Pearce and O'Shea 2007; Bartonicka 2010; Postawa et al. 2014). Thus roost switching may also serve to interfere with mite populations by subjecting them to fluctuating environmental conditions.

Roost microclimate and thus roost switching are also affected by roost structure, together with changes in ambient conditions and reproductive condition of bats. For example, conditions inside caves are typically more stable compared to buildings, which are in turn more stable compared to tree and rock cavities or foliage that vary in accord with ambient conditions (Kunz and Lumsden 2003; Postawa and Gas 2009). Correspondingly, temperate bats roosting in buildings switch roosts less frequently and often have higher parasite loads than do bats roosting in natural cavities, which in turn switch less frequently and have higher parasite loads than bats roosting in foliage (Lewis 1995; ter Hofstede and Fenton 2005; Patterson et al. 2007). Interestingly, black mastiff bats (*Molossus rufus*) roosting in buildings have lower ectoparasite loads compared to those roosting in natural tree hollows, which the authors attribute to lower contact rates in buildings where more space is available (Esbérard et al. 2005). Independent of roost structure, susceptibility to ectoparasites may also vary across the season with physiology, age, and reproductive condition (Pearce and O'Shea 2007). Many ectoparasites are less likely to attach to torpid bats (Montes et al. 2002; Turbill and Geiser 2006) and do not thrive in high temperatures (Bartonička and Gaisler 2007). Bat immunity also varies with reproductive condition (Christe et al. 2000); in particular, females may be less likely to groom themselves while nursing (Christe et al. 2007), and hairless young are more vulnerable than individuals with hair (Lewis 1995). Studies should therefore consider the time of year and reproductive condition of bats when drawing conclusions about roost-switching behaviors.

The relationship between roost-switching and ectoparasite loads is likely to be further complicated by phylogeny, group size, and species-specific behavior. Closely related bat species may be more likely to host similar ectoparasites and use similar roosts, thereby potentially exaggerating the relationship between roost-switching and ectoparasite loads (ter Hofstede and Fenton 2005). However, evidence that conspecifics using different types of roosts (e.g., big brown bats, *Eptesicus fuscus,* use tree cavities, rock cavities, and buildings) have different ectoparasite loads (Patterson et al. 2007; reviewed in Lewis 1995) and different rates of roost switching (reviewed in Lewis 1995) suggests the connection between ectoparasites and roost switching is not simply the result of phylogenetic inertia. Instead, differences in parasite loads across species and conspecific groups in different roosts may reflect group size. Transmission rate may be higher in larger groups typical of caves and buildings compared to smaller groups in foliage roosts (ter Hofstede and Fenton 2005). Larger groups also promote warmer microclimates that favor some ectoparasites (Postawa and Szubert-Kruszyńska 2014). Within groups, individuals may not be equally vulnerable to parasites: more exploratory group members may be more susceptible (Webber et al. 2015). In conclusion, roost switching may serve to reduce ectoparasite loads. However, the likelihood of switching roosts in response to ectoparasites within and across bat species should be expected to vary according to the types of ectoparasites and roosts being considered, geographic location and time of year, and group size and reproductive condition of the bat species under consideration.

4.1.4 Roost Suitability

It is often suggested that bats may switch roosts to locate alternative roosts for future inhabitation (e.g., Kerth and Reckardt 2003; Carter and Feldhamer 2005; Russo et al. 2005). Such scouting could be a very costly endeavor. For instance, because roosts are susceptible to decay or destruction, bats may have to move among several potential roosts to locate a subset of relatively safe, alternative roosts. Indeed, Bechstein's bats living in more dynamic groups discover and occupy newly available roosts more quickly compared to brown long-eared bats living in more cohesive groups (Fleischmann and Kerth 2014), suggesting roost switching, and thus fission–fusion dynamics, may help bats locate new roosts. However, it has been suggested that a bat must spend at least 1 day in a particular roost to assess its suitability (Kerth et al. 2001a, b). As Kerth et al. (2001a, b) suggest, individuals face the risk of spending time in suboptimal conditions that could lead to increased energetic expenditure and reduced offspring survival. It therefore seems unlikely bats switch roosts simply to gather information about alternative roosts for potential future use.

Instead, bats may leave a roost as it becomes unsuitable, either because the structure is no longer available or conditions in the roost have changed for the worse. Certainly roost permanence and microclimate influence roost use by bats. Caves and buildings, on the one hand, are relatively permanent roosts that offer relatively stable microclimates, together with several alternative microclimates in the same roost thus reducing the need to switch roosts (Lausen and Barclay 2006). Crevices in rocks and trees, on the other hand, are subject to decay (Kunz and Lumsden 2003; Barclay and Kurta 2007) and, although microclimate inside these structures is more stable compared to external conditions, microclimate varies to some degree with changes in ambient conditions as well as roost structure (Sedgeley 2001; Clement and Castleberry 2013). Meanwhile foliage is typically ephemeral and the microclimate is strongly influenced by ambient conditions (Kunz and Lumsden 2003). As discussed above, bats switch less frequently among more permanent roosts, such as caves and buildings, compared to bats roosting in trees and foliage (Kunz and Lumsden 2003; Barclay and Kurta 2007). At the same time, however, it is generally thought more permanent roosts are typically more limited on the landscape compared to more ephemeral roosts, which in turn may limit opportunities for roost switching (Lewis 1995). Interestingly, the opposite is true of some tent-making bats; depending on the plant species and mode of construction, some tents can last 6 weeks while others last only days yet bats roosting in more stable tents generally live in more dynamic groups (Sagot and Stevens 2012). That said, within species using similar types of roosts, roost switching is in fact more frequent when roosts are more abundant compared to when roosts are limited in a managed landscape (e.g., Chaverri et al. 2007). Thus, at least for some species, roost permanence and availability influence roost switching.

Examples from vespertilionid bats, where roost switching is particularly well studied, suggest that they switch roosts in response to changes in roost suitability. Soprano pipistrelles move among alternative locations within attics and roofs when temperatures exceed 40 °C (Lourenço and Palmeirim 2004). Similarly, big brown bats switch among buildings primarily on hot days (Ellison et al. 2007). Northern long-eared bats switch among tree cavities almost daily in response to changes in temperature, wind, precipitation, and barometric pressure, but only if they are in trees that are presumably less buffered against fluctuations in ambient conditions (Patriquin 2012). By contrast, pallid bats do not appear to switch roosts in response to daily changes in temperature (Lewis 1996). Meanwhile, the number of bats in a roost affects roost microclimate, arguably to a greater degree than ambient conditions (e.g., Willis and Brigham 2007; Pretzlaff et al. 2010; but see Bartonička and Řehák 2007) yet individual benefits gained through group warming diminish as group size increases (Boyles et al. 2008). Group size will therefore fluctuate as individuals join or leave in an effort to seek an optimal group size (Krebs and Davies 1995). Roost suitability is therefore a dynamic quality influenced by synergistic effects of roost structure, ambient conditions, and the number of bats, which together may explain why bats switch roosts.

4.2 Why Do not Group Members Move Together?

Fission–fusion dynamics in bats are not only the result of roost switching, but more importantly the result of group members switching to different roosts at different times. It therefore seems unlikely that efforts to reduce predation or parasitism can explain why some individuals remain in a roost after part of the group has left, or why a group splits up to move to two or more separate roosts (e.g., Barclay 1982; Lewis 1996; Carter and Feldhamer 2005; Patriquin et al. 2010). Presumably all group members would benefit equally from reduced predation risk and parasitism and would gain these benefits if they moved together to the same roost (Barclay and Kurta 2007). However, group members may not move together if they have different information about roost suitability, including the risk of predation and parasitism. Furthermore, and as noted above, individual costs (e.g., predation and parasitism) and benefits (e.g., group warming and cooperation) of group living also vary dynamically with group size, along with individual differences in sex, age, and reproductive condition (Krause and Ruxton 2002; Terrien et al. 2011). Group members may experience different perceived costs and benefits of remaining in a group, or in moving to one particular roost, and therefore may not move together.

It may be necessary or beneficial for groups to temporarily split into smaller groups (Kerth 2010). For example, space inside roosts may be limited and may force a colony to split into multiple groups, as supported by observations of increasing group size with increasing tree diameter and cavity size (e.g., Lacki and Schwierjohann 2001; Willis et al. 2006; Olson and Barclay 2013). However, this pattern is not consistent across all species, as no relationship between group size and tree diameter was found for northern long-eared bats (Vonhof and Wilkinson 1999). That said, tree diameter may not be a reliable proxy for cavity size in some tree species and therefore may not predict group size (Willis et al. 2006). More than this, based on direct measures of cavity size, Willis and Brigham (2004) argue that the cavities they studied could have supported larger groups of female big brown bats than observed. Thus, it appears that limited space in roosts does not entirely explain why group size changes.

Instead, fission–fusion dynamics likely reflect individuals' attempts to balance the costs and benefits of group living by adjusting group size (Olson and Barclay 2013). For example, the benefits of group warming diminish in larger groups while costs, such as competition, parasitism, and overheating, increase with group size (Olson and Barclay 2013 and references within). Group size is therefore expected to change as the relative costs and benefits of joining a group change, as supported by a direct relationship between group size, roost temperature, and ambient conditions for female temperate bats like Bechstein's bats and big brown bats (Kerth and König 1999; Willis and Brigham 2007; Pretzlaff et al. 2010). This, however, fails to explain why group composition varies almost daily as the same subset of group members could presumably remain together with each fission event, suggesting additional factors influence group composition.

Theoretical evidence suggests group fission and corresponding changes in group composition occur when group members do not reach a consensus on when and where to move (Aureli et al. 2008; Sueur et al. 2011; Kao et al. 2014). As Sueur et al. (2011) point out, individual differences in preferences for when to move could theoretically be resolved by effectively taking the average preference across group members. It remains unclear when the decision is made to switch roosts: dawn swarms (Naďo and Kaňuch 2013) suggest the decision may be made in the morning, while other evidence suggests bats visit roosts throughout the night (Fleischmann and Kerth 2014). Regardless, taking an average decision on whether to move today or several days later could be very costly for bats (see above). Furthermore, it may be difficult to resolve conflict over where to move because spatial location attributes, such as patches of food, water, or shelter, cannot simply be averaged (Sueur et al. 2011). However, while roosts are discrete in space and therefore cannot be averaged, groups could theoretically choose a roost with conditions that best meet the average needs of all group members. Selecting an average roost may, however, result in costly, suboptimal conditions for some group members. Failure to reach group consensus may therefore occur when individual needs conflict with the needs of other group members.

Failure to reach a consensus on when and where to move may also occur when group members have different information about roost suitability. For example, female Bechstein's bats collectively choose to abandon a roost when the majority of group members (more than 50 %) experience a simulated disturbance at the roost (e.g., blocked entrance or a puff of air; Kerth et al. 2006; Fleischmann et al. 2013; Fleischmann and Kerth 2014). However, initial consensus aside, some of these females then chose to return to disturbed roosts (Kerth et al. 2006; Fleischmann et al. 2013; Fleischmann and Kerth 2014). Moreover, Bechstein's bats do not reach group consensus about abandoning a roost when only a minority (less than 50 %) of the group experiences a simulated disturbance at the roost (Kerth et al. 2006; Fleischmann et al. 2013; Fleischmann and Kerth 2014). Interestingly, female brown long-eared bats (*Plecotus auritus*) generally switch roosts less often and always reached a consensus to avoid a roost even when only a minority of group members were presented with an aversive stimulus (an air puff), and in turn live in more cohesive groups (Fleischmann and Kerth 2014). It therefore appears that fission–fusion dynamics occur (i) when individual information conflicts with social information about roost suitability (Kerth 2010; Fleischmann et al. 2013; Fleischmann and Kerth 2014) and (ii) when different individuals have different requirements, due to, for example, differences in age, sex, parasite load, and reproductive condition.

4.2.1 Social

Moving freely among groups and group members should allow bats to maintain social connections across a larger network of group members, thereby increasing their opportunities to cooperate, or share information, with more individuals

(O'Donnell and Sedgeley 1999; Willis and Brigham 2004; Kerth and Van Schaik 2011). Theoretical predictions suggest living within diverse groups facilitates learning (Sueur et al. 2011). Network analyses for giant noctule bats (*Nyctalus lasiopterus*), northern long-eared bats, and Indiana bats have revealed that even group members that roost together only intermittently maintain social connections that may facilitate information flow (Fortuna et al. 2009; Patriquin et al. 2010; Silvis et al. 2014a). Both white-striped free-tailed bats and false vampires appear to increase their networks by roosting with different conspecifics at day roosts than they do at night roosts, as groups of conspecifics found in separate day roosts can be found together at night roosts (Rhodes 2007; Schmidt 2013).

4.3 Do Bats Form Social Bonds Despite Frequent Roost Switching?

To establish whether animals, including bats, with labile group dynamics live in passive aggregations or fission–fusion societies, we must establish whether group members form social bonds. The important distinction is that benefits derived in passive aggregations, such as risk dilution, increased vigilance, reduced energetic costs of movement, or enhanced thermoregulation, depend primarily on the number of group members and interaction among group members is more or less random or restricted to nearest neighbors (reviewed in Kao et al. 2014). By contrast, individuals living in social groups gain additional fitness benefits through cooperation and nepotism by interacting repeatedly with known individuals who may also be related (Kerth 2010). Thus, establishing whether bats form social bonds despite frequent roost switching allows us to differentiate between passive and social groups.

Here we define social bonds (i.e., affiliative social relationships) as nonrandom associations. Through labor-intensive radio tracking and the adoption of microchip technology, the amount of time individuals spend together in day roosts can be measured and compared to a random distribution of associations to determine if associations are truly social or a byproduct of mutual roost preferences (reviewed in Johnson et al. 2013). From this work, it is now evident that group members form preferred associations that cannot be explained by mutual roost preferences, with some group members forming stronger, more lasting relationships than others (Table 4.1). In fact, increasing evidence suggests that, much like other taxa with fission–fusion dynamics, several bat species appear to live in closed societies. Members of sympatric colonies of female Bechstein's bats, big brown bats, and northern long-eared bats, for example, are rarely found roosting together (Kerth et al. 2000; Willis and Brigham 2004; Patriquin et al. 2010). Indeed, female Bechstein's bats may even actively reject foreign conspecifics from roosts (Kerth et al. 2002a, b). Bats therefore appear to form social bonds despite frequent movements among roosts and roost groups.

Not only do some bats form nonrandom associations, these relationships can last for years. For example, Spix's disk-winged bats, a tropical species that roosts in unfurling leaves, maintain preferred associations for at least 100 days, and up to 4 years (Vonhof et al. 2004). Several vespertilionid species in temperate regions all maintain preferred associations across multiple years even though they move to hibernacula for the winter (Patriquin et al. 2010; Kerth et al. 2011; August et al. 2014). Thus, bats form social bonds that can last years, suggesting the potential for cooperation among group members.

The persistence of these bonds has likely played a role in shaping the complex structure of colonies with fission–fusion dynamics. Evidence from Bechstein's bats, Spix's disk-winged bats, big brown bats, and northern long-eared bats, for example, suggest sympatric groups form socially distinct colonies, where conspecifics in one colony are rarely found roosting in adjacent colonies (Kerth et al. 2000; Vonhof et al. 2004; Willis and Brigham 2004; Patriquin et al. 2010). Colonies are therefore made up of a network of groups interconnected by the movement of individuals that in turn form social bonds. Cluster analyses and network analyses suggest subgroups of individuals collectively spend more time together over the summer compared to other group members, resulting in communities within a colony (Patriquin et al. 2010; Kerth et al. 2011). Thus bats with fission–fusion dynamics appear to live in colonies made up of multiple, interconnected subgroups or communities, within which group members form social bonds with each other.

4.4 What Shapes Social Bonds?

Understanding who is more likely to roost together may offer clues as to why we see labile groups, as well as who is more likely to cooperate within these groups. Based on kin selection theory, we might expect close relatives to form stronger social bonds, which may then facilitate nepotism (Hamilton 1964). Indeed various species with fission–fusion dynamics appear to live in matrilineal colonies (Burland et al. 1999; Kerth et al. 2000; Castella et al. 2001; Metheny et al. 2008a; Flanders et al. 2009; Kerth and Van Schaik 2011; Patriquin et al. 2013). In addition, it appears that new colonies of Bechtein's bats and big brown bats are formed when matrilineal kin leave an existing colony to establish a new colony (Kerth 2008b; Metheny et al. 2008b), suggesting a preference to roost with relatives. Within colonies, at least some female Bechstein's bats and northern long-eared bats with the strongest social bonds are also more closely related (Kerth et al. 2011; Patriquin et al. 2013). However, relatedness does not appear to explain social bonds in all colonies of Bechstein's bats, nor in colonies of big brown bats (Kerth and König 1999; Metheny et al. 2008a; Kerth et al. 2011). Instead, the relative importance of relatedness in shaping social bonds may depend on group size or the relative stability of groups; bats in smaller or more stable groups may be able to rely on familiarity, but in larger or more variable groups may have to use additional cues, such as relatedness (Patriquin et al. 2013). Even in systems where relatedness does predict social bonds, females regularly roost with unrelated group members (Kerth et al. 2011; Patriquin et al. 2013). Relatedness therefore does not entirely explain social bonds in these dynamic systems.

We might also expect group members with similar demographics (e.g., reproductive condition and age), and therefore similar needs, to form social bonds. On average, female big brown bats and northern long-eared bats form stronger social bonds at different points in the summer corresponding to reproductive periods (e.g., gestation or lactation), suggesting bonds may be based in part on similar needs during these periods (Willis and Brigham 2004; Garroway and Broders 2007; Patriquin et al. 2010). However, females may not reproduce every summer and the synchrony of parturition varies across species and region, therefore some groups may be comprised of females in different reproductive states (Altringham 1996). Within these mixed groups, Bechstein's bats in the same reproductive condition form stronger relationships (Kerth and König 1999), also suggesting bonds may be based on similar reproductive needs. However, reproductive and nonreproductive female Bechstein's bats are regularly found roosting together (Kerth and König 1999; Kerth et al. 2011) and pairs of nonreproductive and pregnant big brown bats spent more time together than pairs of pregnant bats, suggesting social bonds are not based entirely on similar needs driven by reproduction (Willis and Brigham 2004). It also appears that social bonds are not based on preferences to associate with cohort members. For instance, *Myotis* spp. groups consist of a range of ages (Patriquin et al. 2010; Kerth et al. 2011) and no significant correlation was found between age and association for female Bechstein's bats (Kerth et al. 2011) while older female northern long-eared bats spend more time with younger adult group members (Patriquin et al. 2010). Shared demography thus does not entirely explain social bonds among bats in fission–fusion systems.

It therefore appears that groups may form initially due to similar needs, but within these groups bats may form social bonds based on something more than similarity (Sueur et al. 2011). Like primates, it is possible that social relationships among bats living in fission–fusion systems are shaped by a combination of partner fidelity, or time spent together, and partner choice based on long-term "bookkeeping" of social interactions that may predict the likelihood of receiving cooperative behaviors (Schino and Aureli 2009; Campenni et al. 2015). Longer term studies, such as the work on Bechstein's bats, are therefore necessary to better examine what shapes long-term relationships among bats.

4.5 How Are Social Bonds Maintained?

As in other taxa, long-term social relationships are no doubt facilitated through spatial cues together with mechanisms for individual and kin recognition (Krebs and Davies 1995). For instance, Bechstein's bats, northern long-eared bats, and Indiana bats show interannual fidelity to summer roosting areas and specific roost trees which could allow summer colonies to reestablish social relationships when they come out from hibernation (Kerth and König 1999; Patriquin et al. 2010; Silvis et al. 2014a). Interannual fidelity to roost sites and particular roosts have been documented in various other species and therefore the long-term stability of social relationships in these species warrants further investigation (Barclay and Brigham 2001; Entwistle et al. 2000; O'Donnell 2000; Veilleux and Veilleux 2004; Willis and Brigham 2004; Arnold 2007). While site and roost fidelity may provide a means to locate and recognize group members, it may not allow individuals to reliably differentiate among group members, which would presumably be beneficial in affiliative relationships.

Given most bats rely heavily on echolocation to gain information about their environment; it is not surprising that vocalizations also play an important social role (reviewed in Kanwal et al. 2013 and Schmidt 2013). At least some bats can readily differentiate between conspecific and heterospecific calls at roosts (e.g., Schöner et al. 2010; Furmankiewicz et al. 2011). More importantly, however, several species produce group-specific echolocation and social calls that may allow individuals to differentiate between familiar and unfamiliar conspecifics, as well as individually distinct calls that may allow individuals to differentiate between familiar and unfamiliar group members (Pfalzer and Kusch 2003; Carter et al. 2008; Kazial et al. 2008; Melendez and Feng 2010; Schöner et al. 2010; Voigt-Heucke et al. 2010; reviewed in Carter and Wilkinson 2013a, b and Ross and Holdereid 2013). Evidence from common pipistrelles suggests different matrilines produce different calls that are not likely coded for by mtDNA and are therefore most likely learned from group members (Fornůsková et al. 2014). Vocalizations therefore appear to play an important role in group and individual recognition.

Behavioral evidence also supports predictions that bats use calls to differentiate between familiar and unfamiliar conspecifics. For instance, Spix's disk-winged bats use social calls to maintain contact with group members while foraging (pers. obs. as cited in Chaverri et al. 2012), which may be akin to "grooming at a distance" in primates where group members that regularly groom one another maintain vocal contact when they are apart while foraging (reviewed in Dunbar and Shultz 2010). Maintaining contact while foraging may help bats ensure they later roost with preferred group members (Chaverri et al. 2012). In experimental studies, white-winged vampire bats (*Diaemus youngi*) engage in antiphonal calling when separated from group members and are capable of discriminating between familiar and unfamiliar conspecifics (Carter et al. 2008, 2009). Similarly, pallid bats are more likely to respond to playback calls of familiar group members at roosts (Arnold and Wilkinson 2011). Spix's disk-winged bats in roosts produce "contact" calls in response to "inquiry" calls produced by group members flying in the area who then preferentially enter roosts of familiar group members (Chaverri and Gillam 2010; Chaverri et al. 2010, 2012). Thomas' fruit-eating bats (*Dermanura watsoni*) and Honduran white bats (*Ectophylla alba*) also produce social calls at roosts (Gillam et al. 2013), and giant noctule bats and Daubenton's bats (*Myotis daubentonii*) are attracted to playbacks of conspecific calls at roosts (Ruczyński et al. 2007, 2009), but whether they are used in group recognition remains to be tested.

Visual and olfactory cues may also allow group members to locate one another. For instance, swarming outside summer roosts documented for several species may serve to visually signal the location of group members (Russo et al. 2005; Kerth et al. 2006; Rhodes 2007; Lučan and Radil 2010; Naďo and Kaňuch 2013). Within roosts, olfaction may play an important role in group and individual recognition (Wilkinson 1986; Brooke 1997; Safi and Kerth 2003; Carter and Wilkinson 2013a, b). Gland secretions differ between Bechstein's bat colonies, as well as among individuals within colonies (Safi and Kerth 2003). This, together with evidence that bats rub noses, particularly when they return to a roost, suggests odor cues may facilitate group and individual recognition in this species (Kerth et al. 2003; Safi and Kerth 2003). Additionally, experimental results suggest a range of species living in fission–fusion systems, including common pipistrelles, big brown, and Brazilian free-tailed bats (*Tadarida brasiliensis*), are capable of using olfactory cues to differentiate between familiar and unfamiliar conspecifics (De Fanis 1995; Bloss et al. 2002; Englert and Greene 2009), as well as to differentiate between different familiar group members (De Fanis 1995). Ancillotto and Russo (2014) suggest European free-tailed bats (*Tadarida teniotis*) use olfactory cues to differentiate between familiar and unfamiliar conspecifics, as evidenced by aggressive behavior toward unfamiliar conspecifics. Thus it appears bats may use a combination of spatial, vocal, visual, and olfactory cues to locate group members and maintain social bonds.

4.6 Are There Examples of Cooperation Among Bats Living in Fission–Fusion Systems?

As demonstrated in a recent review (Carter and Wilkinson 2013a, b), there is mounting evidence that bats benefit from cooperative behavior, such as social warming, social grooming, and social transmission of information about roosts and food. It is widely assumed that group warming is the primary benefit of group living in bats (Kerth 2008a), which is presumably dependent more on group size than group composition. However, nonreproductive Bechstein's bats and big brown bats can be found roosting with reproductive conspecifics even though they are under different thermoregulatory constraints and should therefore select different roosts, suggesting they are in fact cooperating to contribute to group warming (Kerth and König 1999; Willis and Brigham 2004). Though studied more extensively in species that live in relatively stable social groups, such as common vampire bats and Kuhl's pipistrelles (*Pipistrellus kuhlii*), social grooming (allogrooming) has also been documented in Bechstein's bats that live in fission–fusion systems (Kerth et al. 2003; Ancillotto et al. 2012; Carter 2015; reviewed in Carter and Wilkinson 2013a, b). Social grooming in these dynamic systems may help build and maintain social bonds as it does in a range of other taxa (reviewed in Dunbar and Schultz 2010 and Russell and Phelps 2013).

Bearing in mind that bats can live up to 30 years or more, and females show strong natal philopatry to summer breeding areas and to roosts, it is possible they could build long-term knowledge about suitable roosts and share this information with younger, less experienced group members. Experimental evidence suggests bats are indeed capable of remembering spatial cues (reviewed in Ross and Holderied 2013) and theoretical models suggest remembering the location of roosts reduces search effort (Ruczyński and Bartoń 2012). Field observations of bats swarming outside roosts before entering for the day (Russo et al. 2005; Kerth et al. 2006; Rhodes 2007; Lučan and Radil 2010; Naďo and Kaňuch 2013) together with evidence of antiphonal calling by Spix's disk-winged bats at roosts (Chaverri et al. 2010, 2012) and experimental studies demonstrating that experienced female Bechstein's bats return to roosts with naïve group members prior to choosing a roost for the day (Kerth et al. 2006; Fleischmann et al. 2013; Fleischmann and Kerth 2014), suggest bats have the opportunity to learn about suitable roosts from group members.

Bats living in fission–fusion systems may also learn about foraging opportunities from group members. Several studies have demonstrated that bats from a range of social systems, including little brown bats, big brown bats, and Brazilian free-tailed bats that live in fission–fusion systems, can learn about food availability, and how to capture prey, through auditory, visual, and olfactory cues (Gaudet and Fenton 1984; Ratcliffe and ter Hofstede 2005; Page and Ryan 2006; Gillam 2007; Dechmann et al. 2009, 2010; Wright et al. 2011; Jones et al. 2014; O'Mara et al. 2014). However, it is possible that only species feeding on patchily distributed food, such as fruit or insect swarms, are likely to benefit from information sharing compared to gleaning species that feed on single prey, rather than patches, that are typically distributed less predictably.

Alloparental care, such as nursing and guarding nondescendant pups, has also been documented in bats. However, examples of these behaviors are restricted to species that live in year-round stable groups, including evening bats (*Nycteris humeralis*) (Wilkinson 1992; reviewed in Carter and Wilkinson 2013a, b) and greater spear-nosed bats (*Phyllostomus hastatus*) (Bohn et al. 2009; reviewed in Carter and Wilkinson 2013a, b). It therefore appears strong, predictable bonds may be needed to offset the costs of investing energy in nondescendant young.

4.7 What Does All of This Tell Us About Evolution of Fission–Fusion Dynamics?

Consistent with evidence from primates, cetaceans, and elephants, work with bats supports theoretical predictions that, like other social systems, fission–fusion dynamics are influenced by life history, reproductive strategy, phylogeny, and resource stability (Clutton-Brock and Janson 2012). For instance, fission–fusion has evolved primarily in long-lived animals with high offspring investment and high female philopatry occupying environments that vary within an individual animal's lifetime (Aureli et al. 2008; Couzin and Laidre 2009). Together, these characteristics favor group living, cooperative behavior, and social learning to better adapt to changes in the environment (Whitehead 2007; Aureli et al. 2008). Moderate spatial and temporal variability then leads to changes in the relative costs and benefits of group living, resulting in fission–fusion dynamics with some level of consensus among group members (Sueur et al. 2011). This is consistent with the observation that fission–fusion dynamics predominate in bats living in temperate regions where there are both seasonal and daily fluctuations in the environment. By contrast, year-round stable groups predominate in the tropics where conditions are less variable. Of course, as highlighted above, there are exceptions: several tropical species, including Spix's disk-winged bats and some tent-roosting bats, do live in fission–fusion systems. These species, however, tend to rely on ephemeral roosts which may necessitate roost switching; at the same time, despite frequent roost switching, tent-making species studied to date form groups that are relatively more stable compared to temperate bats. Predictions about resource stability and its influence on group structure therefore require further testing.

Consistent with theoretical predictions and empirical evidence from elephants and primates (Aureli et al. 2008), it appears that fission–fusion systems in bats favor individual recognition over group signatures. For example, species living in fission–fusion systems, such as Spix's disk-winged bats, produce individually specific calls rather than group-specific calls (Gillam and Chaverri 2012). By contrast, species living in stable social groups, such as greater spear-nosed bats and lesser bulldog bats (*Noctilio albiventris*), rely on group-specific calls, with some also using individually distinct calls (Boughman 1997; Boughman and Wilkinson 1998; Voigt-Heucke et al. 2010). Moreover, scent profiles differ between colonies of Bechstein's bats, but also across individuals within colonies (Safi and Kerth 2003). Thus, it appears individual recognition may be more important in fission–fusion systems where group members interact intermittently compared to stable groups where group members interact predictably.

4.8 Conclusions and Future Directions

Fission–fusion societies in bats appear to consist of colonies made up of multiple interconnected subgroups or communities consisting of multiple matrilines, within which group members form social bonds with each other based in part on relatedness and similarities in reproductive condition. The fundamental driver of these fission–fusion dynamics is frequent roost switching, likely due to a combination of predation risk, commuting costs, ectoparasitism, and changes in roost availability. Group composition changes when group members switch to different roosts at different times, likely due to benefits of temporarily splitting into smaller groups together with lack in group consensus on when and where to move. Despite the fluid nature of these groups, bats maintain long-term social bonds that may then favor the evolution of cooperation among group members. However, more work is needed to better understand both the proximate and ultimate causes of fission–fusion dynamics in bats, which we highlight below with suggestions for future work.

The causes of roost switching require closer examination. Most studies have approached the question of roost switching as a univariate problem, when in reality factors such as predation risk, commuting costs, and ectoparasites are likely not mutually exclusive and their relative influence will depend on the synergistic effects of roost type, environment, and demography. Ellison et al. (2007) suggested the strong effect of temperature on roost switching by big brown bats may have masked the effect of ectoparasites. Moreover, the influence of each of these factors will no doubt differ for bats roosting in foliage compared to those roosting in caves or buildings, due to differential exposure to predators, parasites, and the elements. For example, pallid bats using roosts with different characteristics show different roost-switching behavior and correspondingly different ectoparasite loads (reviewed in Lewis 1995). Similarly, the degree of roost switching varies with reproductive condition, due in part to physical constraints on movement when pregnant and transporting nonvolant young, but also due simply to differences in thermoregulatory demand. Thus, the costs of moving may simply outweigh the benefits of switching roosts during certain periods. Future studies should therefore expand on the work of Ellison et al. (2007) by quantifying all possible factors, including predator densities, ectoparasite loads, distances between roosts and feeding sites, changes in ambient conditions, and corresponding changes in roost quality. Furthermore, to better examine proximate factors shaping fission–fusion dynamics, researchers should use multivariate analyses to examine the relative effect of each factor while controlling for reproductive condition.

The influence of predation risk and ectoparasites on roost switching requires more careful examination to better assess their role in the evolution of fission–fusion dynamics. In particular, controlled experiments that manipulate predation risk and field studies that provide estimates of predator densities could help clarify the role of predation risk on roost switching (see Lima and O'Keefe 2013 for a detailed discussion of the effect of predators on bat behavior, and how to test these effects). Concurrently, efforts should be made to quantify all ectoparasites because strategies to reduce ectoparasites differ for mites and bat flies (ter Hofstede and Fenton 2005; Postawa and Furman 2014; Postawa et al. 2014). Further, experimental studies similar to that of Reckardt and Kerth (2007), which manipulated ectoparasite loads in roosts, would also help quantify the effect of parasites on roost-switching behavior. As with any rigorous study, a sufficient number of group members must be examined to account for individual variation, which may be particularly important in light of recent evidence that susceptibility to parasites varies with age, sex, and exploratory behavior (Webber et al. 2015).

The influence of ambient conditions on roost-switching behavior also requires more attention. For example, more studies from across a range of species and conspecifics occupying roosts that differ in vulnerability to changes in ambient conditions (e.g., buildings, trees, and foliage) would help determine whether environmental variability does in fact shape fission–fusion dynamics. Also, experimental manipulation of temperatures in bat boxes could provide valuable insight to the influence of microclimate on roost switching. To date, manipulations of bat boxes have demonstrated that bats prefer warmer roosts during lactation (Kerth et al. 2001a, b). This work could be expanded using a thermostat to regulate a constant optimal temperature inside bat boxes where bats would presumably remain for the entire season if changes in roost microclimate are the only predictors of roost switching. Also, creating a set of roosts where each have different temperatures could determine whether group consensus could be achieved if an "average" roost were available or whether it would still be too costly for some group members to move to a suboptimal roost.

Change in group size and composition after switching roosts is, of course, also fundamental to the evolution of fission–fusion dynamics. It appears that group size and composition change when it is beneficial to temporarily split into multiple smaller groups to offset the costs of group living and when group members cannot come to a group consensus on where to move (Kerth 2010). These conclusions, however, have been drawn based largely on work with a single species, Bechstein's bats, living in bat boxes. Recent evidence of strong interspecific differences in group cohesion (Fleischmann and Kerth 2014) highlights the need for more extensive studies examining group consensus across a range of species and conspecific groups in different environments and that use different types of roosts. Fleischmann and Kerth (2014) suggest future work should also consider social and genetic relationships and how they affect the likelihood of reaching a group decisions as individuals with stronger social or genetic ties may be more likely to reach consensus. Behavioral syndromes may also influence decision-making (Fleischmann and Kerth 2014). Kilgour and Brigham (2013) experimentally demonstrated that some group members are more likely than others to explore and discover new food resources. Perhaps more exploratory individuals are more likely to leave group members to locate new roosts while others are more likely to stay behind, as suggested for Bechstein's bats (Kerth and Reckardt 2003) and giant noctule bats (Fortuna et al. 2009). As future work clarifies the causes of fission–fusion dynamics, we can then better test hypotheses that fission–fusion dynamics allow group members to balance individual needs with the costs and benefits of group living (Kerth 2010).

Despite the fluid nature of these groups, individuals form both short- and long-term bonds. These bonds appear to be based in part on relatedness and shared needs shaped by similarities in reproductive condition. However, evidence that unrelated individuals and females in different reproductive condition form bonds suggests bonds are shaped by more than shared needs. Future work could expand on a recent experiment that provided big brown bats a binary choice between pairs of known conspecifics (Kilgour et al. 2013). Interestingly, a recent study suggests that early association shapes social bonds as juvenile Kuhl's pipistrelles that roost close together form long-term relationships in adulthood (Ancillotto et al. 2012), which may then also explain why some group members remain together despite fission–fusion events. As discussed by Aureli et al. (2008), communication is also a key to group dynamics. Thus, more explicit tests are needed to examine how group members find each other. Relocation experiments similar to an experiment performed by Willis and Brigham (2004), for example, could prove valuable.

In their review, Dunbar and Schultz (2010) point out that within a social system, there are likely different levels of organization that may be akin to hierarchies. Indeed, within colonies of Bechstein's bats and northern long-eared bats, distinct communities or subgroups exist where females are more likely to interact with one another compared to other group members (Patriquin et al. 2010; Kerth et al. 2011). Dunbar and Schultz (2010) therefore suggest that the level of social complexity can be compared across species by quantifying the size of the "base unit" (i.e., a summer colony of bats) and "the number of layers of acquaintanceship that emerge from it" (i.e., subgroups or communities in bats) (p. 795). Living in closed societies can be both beneficial and costly, as discussed in more detail by Kerth and Van Schaik (2011). For instance, living in closed societies consisting primarily of maternal kin may favor cooperation and nepotism and it appears to limit exposure to novel pathogens (Kerth and Van Schaik 2011). At the same time, however, these authors (Kerth and Van Schaik 2011) suggest bats in closed societies may not be able to disperse to new roosting areas following a disturbance, particularly given foreign individuals may be actively excluded from roosts (Kerth et al. 2002a, b). However, the case where socially distinct groups of Bechstein's bats fused to form a single group following a population crash further refutes this hypothesis (Baigger et al. 2013).

Fission–fusion dynamics vary along a continuum, within and across species and over time (Aureli et al. 2008). Brown long-eared bats switch roosts less frequently and therefore live in more cohesive groups compared to Bechstein's bats (Fleischmann and Kerth 2014). When big brown bat and Bechstein's bat colonies become too large, they split into multiple new colonies, where matrilineal kin leave a colony to establish a new colony elsewhere (Kerth 2008b; Metheny et al. 2008b). By contrast, when Bechstein's bat colony size decreased due to a sudden population crash, otherwise socially distinct communities merged (Baigger et al. 2013). Initially group members from each community spent more time with each other but, over time, these former preferred relationships broke down and new bonds formed (Baigger et al. 2013). We hypothesize that group mergers, together with a breakdown of preexisting relationships over time to form new social bonds, may then explain why colonies consist of multiple matrilines and why social bonds within these colonies are not necessarily predicted by relatedness (Kerth and König 1999; Metheny et al. 2008b; Kerth et al. 2011; Patriquin et al. 2013). We also propose that the degree of structuring (i.e., number of communities or subgroups) within a colony, as well as the factors shaping social relationships within colonies, such as relatedness, may differ depending on whether a colony has undergone a large-scale fission into multiple colonies or whether it has formed as a result of the fusion of multiple communities. The structure and relationships within colonies will also depend on the amount of time that has passed since the fission or fusion event. We might therefore expect findings to vary across species and conspecific groups in future studies.

Though evidence is mounting that bats form social bonds in dynamic fission–fusion systems, it is generally assumed that time spent in the same roost translates to social interactions such as cooperation, which may not be the case (Dunbar and Schultz 2010). For instance, at least one study suggests bats may line cavity walls rather than form clusters in roosts (unpublished data as cited in Willis and Brigham 2007), suggesting individuals within a roost do not necessarily interact equally. However, with greater affordability and advances in technology, we encourage future work to document interactions among bats (see Hristov et al. 2013 for a review and suggestions). In addition to suggestions offered by Hristov et al. (2013), we propose future work could mark individuals with a fluorescent powder and quantify the rate of transfer among group members to first establish whether bats roosting together do in fact interact and therefore potentially cooperate. At the same time, care must be taken when interpreting such data as strength of social relationships may not predict cooperation and reciprocity may not be tit for tat: for example, allogrooming may be exchanged for a different service, such as information about food (Carter and Wilkinson 2013a, b).

Network analyses are a valuable tool that can help reveal the complexities of fission–fusion dynamics, as well as the potential for cooperation and information flow among group members (Croft et al. 2008; Whitehead 2008). However, some caution must be exercised when using, and interpreting, these analyses (see Johnson et al. 2013 for suggestions). For instance, theoretical models have demonstrated that fission–fusion can emerge from random patterns as individuals aggregate around a common resource (Cross et al. 2005; Ramos-Fernández et al. 2006). Future work should therefore ensure observed association patterns are compared against random distributions to confirm they represent social preferences rather than shared interest in resources (Whitehead 2008). With proper care, future work could then test predictions about roles of individuals in networks by comparing the rate of spread of novel information among group members with different degrees of direct and indirect connections, or for individuals that may act as “brokers” between subgroups. It would also be interesting to look at reproductive success of females that are more central to networks compared to those at edges: evidence from baboons suggests females that spend more time with other group members, and more time allogrooming, have higher reproductive success (Silk 2007).

Future work should also examine sociality in male bats, which has received little attention. Comparative studies looking at roost switching and ectoparasites in male and female conspecifics, for example, would help tease apart the role of environment and ectoparasites in shaping roost switching and fission–fusion dynamics. Adult male Bechstein’s bats typically switch roosts less often than females and have more bat flies, suggesting more frequent roost switching may in fact serve to reduce parasite load (Reckardt and Kerth 2006).

Relationships at night roosts and hibernacula have also largely been ignored. It remains to be seen whether other species follow patterns similar to false vampires and white-striped free-tailed bats where groups of conspecifics found in separate day roosts can be found together at night roosts (Rhodes 2007; Schmidt 2013). Moreover, as Kerth and Van Schaik (2011) point out, it is not yet known whether groups found roosting together in the summer are also found hibernating together. Hibernating with summer groups could presumably allow bats to maintain the long-term social bonds that have been documented in some species. Bats are regularly aroused through winter in response to evaporative water loss during hibernation (Ben-Hamo et al. 2013 and references within), offering them the opportunity to interact with each other. If, summer groups do also hibernate together this could have devastating consequences in light of the emergence of white-nose syndrome. The rapid spread of this lethal fungus (*Pseudogymnoascus destructans*) throughout hibernacula in eastern North America has resulted in the loss of nearly six million bats since its first detection in 2006 (BCI 2014). If summer social groups also hibernate together and are subsequently lost to white-nose syndrome, we could see the loss of entire matrilines, resulting in reduced genetic variance. Moreover, we could see the loss of entire colonies in a particular area as populations of big brown bats, eastern small-footed myotis (*Myotis leibii*), little brown bats, northern long-eared bats, Indiana bats, and tricolored bats (*Perimyotis tricolor*) are all declining as a result of white-nose syndrome (Langwig et al. 2012). This then raises the question whether summer colonies of each of these species will also merge as observed in Bechstein's bats following a population crash.

Though our understanding of fission–fusion dynamics in bats has grown over the past 15 years, much remains to be learned. Most of what we know is based on only a few well-studied species, and Bechstein's bats in particular, and therefore conclusions are somewhat speculative at this time. As suggested for future directions for work with primates, we should be testing predictions about selection on group structure by performing comparative studies across species that consider ecology and phylogeny, and compare this to work in other taxa (Clutton-Brock and Janson 2012). This highlights the need for more extensive studies across species, as well as across conspecifics occupying different environments and sympatric groups of conspecifics using roosts that vary in stability. Comparative studies of heterospecifics living in different social systems but in similar environments would also help to further understand the evolution of fission–fusion dynamics in bats. Also, as can be seen in Table 4.1, measures of association and definitions of social groups vary widely across studies. We therefore encourage future work to use consistent terminology and methodology to better allow comparisons across studies.

4.9 Conservation Implications

Bats living in fission–fusion systems need a multitude of roosts to support social relationships and thermoregulatory needs (O'Donnell 2000; Willis and Brigham 2004; Russo et al. 2005; Popa-Lisseanu et al. 2008; Fortuna et al. 2009; Patriquin et al. 2010). Previous conservation efforts have endeavored to quantify key roost characteristics to conserve particular types of trees. However, evidence of high reuse of particular trees in some areas together with observations that bats use a large set of roosts within and across years suggests they require a set of roosts with different characteristics (Barclay and Kurta 2007). Some of these roosts appear to act as "central" or "primary" roosts as they are used repeatedly throughout a summer and by more group members than other roosts (Barclay and Kurta 2007; Popa-Lisseanu et al. 2008; Silvis et al. 2014a; Patriquin pers. obs). Loss of these central roosts results in dramatically fragmented social networks for Indiana bats (Silvis et al. 2014a) and the loss of roosts in general could result in smaller home ranges together with smaller colony sizes, in turn increasing the risk of local extinction (Borkin and Parsons 2011, 2014).

Susceptibility to disturbance may also depend on the shape of the network. Simulations suggest Indiana bat networks are more sensitive to roost loss, as networks were fragmented into multiple, smaller groups following the removal of 10 % of roosts, whereas the removal of more than 20 % of northern long-eared bat roosts was needed before colonies became fragmented (Silvis et al. 2014a, b). Colonies were less likely to fragment when bats shared a higher number of roosts (Silvis et al. 2014a). A further test of this could compare the effect of roost loss on Bechstein's bat and brown long-eared bat networks, which exhibit different levels of fission–fusion dynamics and correspondingly different abilities to discover and occupy new roosts (Fleischmann and Kerth 2014). In conclusion, how bats determine whether they should stay or should go is a multifaceted question, one that requires careful attention by researchers to a wide variety of biotic and abiotic factors, and one that likely differs across species, populations, and individuals and varies over time.

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Chapter 5
Sociality, Parasites, and Pathogens in Bats

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Abstract Little is known about the ecology of many of the parasites and pathogens affecting bats, but host social behavior almost certainly plays an important role in bat-parasite dynamics. Understanding parasite dynamics for bats is important from a human public health perspective because of their role as natural reservoirs for recent high-profile emerging zoonotic pathogens (e.g. Ebola, Hendra) and from a bat conservation perspective because of the recent emergence of white-nose syndrome (WNS) in North America highlighting the potential population impacts of parasites and pathogens. Although some bat species are among the most gregarious of mammals, species vary widely in terms of their social behavior and this variation could influence pathogen transmission and impacts. Here, we review the literature on links between bat social behavior and parasite dynamics. Using standardized search terms in Web of Science, we identified articles that explicitly tested or discussed links between some aspect of bat sociality and parasite transmission or host population impacts. We identified social network analysis, epidemiological modeling, and interspecific comparative analyses as the most commonly used methods to quantify relationships between social behavior and parasite-risk in bats while WNS, Hendra virus, and arthropod ectoparasites were the most commonly studied host-parasite systems. We summarize known host-parasite relationships in these three systems and propose testable hypotheses that could improve our understanding of links between host sociality and parasite-dynamics in bats.

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5.1 Introduction

Parasitism is ubiquitous in nature. Parasites affect fitness of their hosts and thus can shape host population dynamics. Defined broadly, a parasite is any organism that grows, feeds, and/or is sheltered at the expense of another organism (i.e. the host). Parasites can be categorized into different ways but one common approach is to differentiate microparasites, which are typically unicellular or multicellular microbes (e.g. bacteria, prions, viruses, protozoans, fungi) with short generation times and a life cycle that occurs entirely on/in the host, from macroparasites which are multicellular parasites with longer generation times and more complex life cycles that may include multiple host species (Table 5.1; Anderson and May 1979; Hudson et al. 2002). Many microparasites can be pathogenic and cause identifiable disease in their hosts with recognizable physiological or behavioral signs or symptoms (Table 5.1). For example, *Batrachochytrium dendrobatiidis* is a fungal microparasite of amphibians that infects keratinized tissues, thickens the epidermis, and eventually causes mortality, all of which are identifiable signs of the associated disease, chytridiomycosis (Voyles et al. 2009; Rosenblum et al. 2010). Macroparasites tend to result in chronic infections of their definitive hosts, decrease host fecundity, and usually cause morbidity rather than mortality (Hudson et al. 2002). Experimental infection of great tits (*Parus major*) with the hen flea (*Ceratophyllus gallinae*) resulted in reduced reproductive success via increased nest failure during incubation and the nestling period (Fitze et al. 2004). Parasite dynamics and impacts are often quantified using two metrics: intensity (i.e. load) and prevalence. Intensity quantifies the number of infections per individual host within a given population, while prevalence is measured as a proportion of infected individuals within a sample from a given host population (Table 5.1). Understanding variation in parasite prevalence and intensity can thus be important for making inferences about the evolution of social behavior and the potential fitness consequences associated with parasite infection.

Although empirical data from wild host populations are surprisingly scarce, host behavior is considered an important predictor of parasite intensity, prevalence, and impacts (Moore 2002). A longstanding hypothesis in parasite ecology predicts an influence of the host social system, and the duration and frequency of social contacts within host populations, on parasite prevalence or intensity (Loehle 1995; Altizer et al. 2003). Social systems, defined as groups of conspecifics that regularly interact more frequently with one another than with members of other groups, represent the highest level of sociality, while social organization and social structure describe the size, composition, and spatiotemporal distribution and cohesion of social systems (Table 5.2; Whitehead 2008). Social systems can be further subdivided into two categories: colonies and aggregations, and this distinction is important for understanding host-parasite dynamics in bats. Colonies are groups of individuals that may or may not be genetically related but which exhibit non-random patterns of association, and frequent close contact with each other (Kerth 2008). It is often assumed that groups of bats roosting in a common structure represent a colony but often such groups may not meet the colony definition and,

Table 5.1 Summary and definitions of commonly used terms associated with parasitism

Term	Definition	Source
Host	An animal or plant on which a parasite lives.	Martin (2010)
Reservoir host (ecological definition)	Hosts that do not exhibit clinical disease as a result of infection.	Nunn and Altizer (2006)
Reservoir host (medical definition)	Hosts that serve as a source of infection and potential reinfection of people and sustain parasite populations when humans are not available.	Martin (2010)
Parasite (ecological definition)	Any organism that lives on and draws nutrients from another living organism (the host), usually to the host's detriment.	Nunn and Altizer (2006)
Parasite (medical definition)	An organism that grows, feeds, and is sheltered on (ectoparasite) or in (endoparasite) a different organism while contributing nothing to survival of its host.	Martin (2010)
Microparasite	Pathogens, or disease-causing microbes (viruses, bacteria, protozoa, fungi).	Anderson and May (1979)
Macroparasite	Multicellular parasites (helminthes, arthropods, most ectoparasites)	May and Anderson (1979)
Disease (ecological definition)	Pathology caused by infection, including outward physical signs and internal or behavioral changes.	Nunn and Altizer (2006)
Disease (medical definition)	A disorder with a specific cause (may or may not be known) and recognizable signs and symptoms.	Martin (2010)
Pathogen	Disease-causing agent.	Nunn and Altizer (2006)
Virulence (ecological definition)	Disease-induced host mortality and/or reductions in fecundity	Nunn and Altizer (2006)
Virulence (medical definition)	The disease-producing (pathogenic) ability of a microorganism.	Martin (2010)
Infection	Invasion of the body by harmful organisms (pathogens), such as bacteria, fungi, protozoa, or viruses.	Martin (2010)
Prevalence	A measure of morbidity based on current levels of disease in a population; measured as a proportion (i.e. number of infections divided by number of individuals).	Martin (2010)
Intensity	A measure of morbidity based on current levels of disease in a population; measured as an absolute number (i.e. the total number of infections).	Martin (2010)
Epidemiology	The science concerned with the study of the factors determining and influencing the frequency and distribution of disease in a defined human or animal population.	Martin (2010)

instead, represent aggregations. Aggregations are defined as assemblages of individuals that happen to occur in a shared environment at the same time, perhaps due to an attraction to that environment rather than social bonds with other individuals (Table 5.2). Variation in social dynamics within and between colonies and aggregations can mediate host-parasite dynamics (Webber et al. 2016).

Table 5.2 Summary and definitions of commonly used terms associated with socioecology and personality in the context of host–parasite interactions of bats

Term	Definition	Source
Social structure	The composition of groups and the spatial distribution of individuals.	Whitehead (2008)
Social organization	Size, sexual composition, and spatiotemporal cohesion of a society.	Whitehead (2008)
Social system	Set of conspecific animals that interact regularly and more so with each other than with members of other such societies.	Whitehead (2008)
Society	A group of individuals belonging to the same species and organized in a cooperative manner.	Wilson (1975)
Colony	Characterization of roosting associations of bats, which may or may not maintain body contact with each other in a communal roost. 'Colony' is commonly used for females breeding communally in maternity colonies.	Kerth (2008)
Aggregation	Anonymous assemblage of individuals at the same place. Bats in aggregations show no social bonds and do not engage in cooperative or other affiliate social interactions.	Kerth (2008)
Gregarious	An individual's tendency to associate with conspecifics.	Godde et al. (2013)
Sociability	An individual's reaction to the presence or absence of conspecifics. Sociability ranges along a continuum and sociable individuals tend to seek the presence of conspecifics while unsociable tend to avoid conspecifics.	Réale et al. (2007)
Activity	The general level of activity of an individual.	Réale et al. (2007)
Exploration	An individual's reaction to a novel object or situation.	Réale et al. (2007)

Relationships between host social systems and parasite dynamics are complex, but several mechanisms are predicted to influence these patterns and are likely important for bats. For example, hosts that occur in large, high-density colonies are predicted to have more frequent interactions resulting in more opportunities for parasite transmission (Stanko et al. 2002; Tompkins et al. 2011). Dense aggregations may result in contacts that are fewer and shorter in duration than those occurring in colonies, but are still likely to provide more opportunities for parasite transmission than might occur for solitary bats or those in very small colonies. This variation in host density also has the potential to influence one of the most fundamental parameters of disease ecology, the basic reproduction number or basic reproductive ratio (R_0). R_0 is an important metric of parasite fitness typically defined, for microparasites, as the number of secondary infections caused by an infectious individual in an entirely susceptible population or, for macroparasites, the number of female larvae established from a single female worm (Hudson et al. 2002). When $R_0 > 1$ infection persists within the host population and when $R_0 < 1$ infection cannot become established (Perkins et al. 2003). Variation in social behavior can impact R_0 if certain individual hosts disproportionately infect a large number of conspecifics, and thus inflate R_0 above the persistence threshold of one (Lloyd-Smith et al. 2005). Although empirical data from numerous vertebrates (e.g. ungulates: Ezenwa 2004) and invertebrates (e.g. bees: Otterstatter and Thomson 2007) support theoretical relationships between parasitism and sociality, there are few data for most host–pathogen systems involving wild mammals, including bats.

Bats are among the most ecologically diverse of mammals with an enormous range of social systems (Kunz and Lumsden 2003; Kerth 2008; Johnson et al. 2013). For example, colony or aggregation sizes of bats range from completely solitary to millions of individuals, while social systems range from small, closed societies with potentially long-term social bonds (e.g. *Thyroptera tricolor*: Chaverri 2010) to enormous, likely passive aggregations of individuals attracted to high-quality habitats (e.g. *Myotis lucifugus* during autumn swarming: Fenton 1969). Social behavior in bats presumably evolved in response to the costs and benefits associated with close conspecific contact. Benefits of social roosting may be numerous and include social thermoregulation, cooperative behavior, and information transfer. Many temperate bats rely on social thermoregulation to decrease energy expenditure during periods of energy limitation, such as pregnancy and lactation (e.g. *Eptesicus fuscus*: Willis and Brigham 2007), while some tropical species also appear to exploit social thermoregulation (e.g. *Uroderma bilobatum*: Lewis 1992). The evolution of cooperative behavior in bats was likely facilitated by strong female philopatry and stable group structure (Emlen 1994). Vampire bats (*Desmodus rotundus*) are well known for their cooperative behavior (i.e. reciprocal altruism) and females rarely transfer between groups (Wilkinson 1987; Carter and Wilkinson 2013). This combination suggests an evolutionary scenario, where stable group structure ultimately led to selection favoring cooperative behavior. Information transfer about predation risk (e.g. Kalcounis and Brigham 1994) and high-quality foraging sites (e.g. McCracken and Bradbury 1981) are also commonly cited as potential benefits of sociality for bats.

Despite these potential benefits of social behavior, risk of infection with micro- and macroparasites is thought to represent a potentially pronounced fitness cost of being social (Côté and Poulin 1995). This cost is illustrated most obviously by the recently emerged infectious disease white-nose syndrome (WNS), which is caused by the fungal microparasite *Pseudogymnoascus destructans* (Blehert et al. 2009). WNS has resulted in catastrophic declines of temperate hibernating bats in North America (Frick et al. 2010) and prompted urgent conservation and management attention (Foley et al. 2011; Fenton 2012). *P. destructans* is an invasive pathogen that appears to have evolved with bats from the old world, where it does not cause mortality of infected hosts, and to date, is known to occur on at least 15 hibernating bat species (Puechmaille et al. 2011; Zukal et al. 2016). *P. destructans* grows in exposed skin of the muzzle, ears, and wing membranes of bats during hibernation (Blehert et al. 2009; Warnecke et al. 2012). For North American species, infection with *P. destructans* causes an increase in energy expenditure (Verant et al. 2014) and arousal frequency (Boyles and Willis 2010; Reeder et al. 2012; Warnecke et al. 2012) which lead to premature depletion of fat stores during hibernation. Although the mechanism inducing increased energy expenditure and arousals by infected bats is still not fully understood (for review see Willis 2015), variation in social behavior could mediate fungal transmission and growth, especially since affected species tend to hibernate in large colonies or aggregations in caves or mines. Understanding host-parasite dynamics in the context of social behavior for WNS is therefore important from a conservation perspective.

In addition to serious conservation threats for some species, bats also appear to be reservoir hosts for a number of emerging infectious diseases (EIDs) of public health concern (Luis et al. 2013; Plowright et al. 2015). Reservoir hosts tend not to exhibit clinical disease as a result of infection (Baker et al. 2013) and reservoir host populations may therefore provide large pools of infected hosts that could facilitate spillover events to heterospecifics, including humans, livestock, or pets (Luis et al. 2013; Plowright et al. 2015). Interestingly, their apparent ability to tolerate infection with a wide diversity of viral parasites is one factor supporting the recent hypothesis that bats are ‘special’ with respect to their propensity to host zoonotic microparasites (Luis et al. 2013; Brook and Dobson 2015). The recent identification of a number of viral, protozoan, and bacterial microparasites in bats supports this hypothesis and has prompted significant analysis and discussion about bats as natural hosts to microparasites associated with EIDs of humans or livestock (Hayman et al. 2013; Luis et al. 2013; Olival and Hayman 2014; Veikkolainen et al. 2014). For example, recent evidence suggests that bats host more zoonotic viruses per species compared to rodents, and human encroachment into bat habitats, particularly in the tropics, could facilitate spillover events (Daszak et al. 2000; Luis et al. 2013). Several hypotheses have been proposed to explain the apparent zoonotic potential of bats. Enormous variation in body temperature (T_b) and metabolic rate (MR) between rest and sustained flight in many heterothermic bats could reduce fitness or pathogenicity for many viral parasites (O’Shea et al. 2014). Interestingly, widespread torpor expression in bats appears to reduce the likelihood of hosting zoonotic viruses, possibly because viral replication decreases as a result of reduced T_b and MR during torpor (Luis et al. 2013; Stawski et al. 2014). This hypothesis suggests physiological tolerance as a mechanism allowing bats to serve as reservoir hosts, but evidence linking host sociality as an additional mechanism is limited (Hayman et al. 2013).

Despite the fundamental evolutionary importance, and conservation and public health significance of bat-parasite interactions, studies of the influence of bat sociality on parasite transmission and acquisition are limited, especially for microparasites. Here, we review the literature on relationships between social behavior of bats and their associated parasites. First, we provide an overview of the tools, techniques, and methodologies that have been used to quantify relationships between sociality and parasitism in bats, as well as relevant techniques that have been used for other vertebrates and which could be applied to bats. Second, we summarize the role of sociality in three relatively well-studied bat-parasite systems: WNS, Hendra virus (HeV), and arthropod macroparasites. Finally, we propose testable hypotheses and observational and experimental studies important for understanding the influence on parasite dynamics of two important concepts in behavioral ecology of bats: fission–fusion social organization and individual behavioral tendencies (i.e. personality).

5.2 Tools, Techniques, and Methodologies

We conducted an extensive search of the literature and compiled a list of articles based on combinations of key word searches on Web of Science. We searched the term "Chiroptera" and "bat" with every possible combination of social*, gregarious*, colony, aggregation, fission–fusion (i.e. a common type of bat social system, see below), viral, pathogen, disease, ectoparasite*, endoparasite*, parasite*, infection* and epidemiology*. Our initial search yielded 223 unique articles but we eliminated articles that did not explicitly quantify or discuss a link between some aspect of sociality and parasite risk. This left only 35 articles that fully satisfied our search criteria. Four of these used comparative analyses to examine effects of species-specific socioecological traits on parasite risk (Table 5.4), 15 addressed sociality in the context of microparasites (Table 5.4), and 16 addressed sociality in the context of macroparasites (Table 5.5).

The studies we identified employed a range of methodologies to quantify links between sociality and parasite risk (Tables 5.3, 5.4 and 5.5). Methods included social network analysis (n = 3), epidemiological modeling (n = 5), and interspecific comparative analyses (n = 4). Details about the underlying theory and the implementation of these methods is available elsewhere (e.g. social network analysis: Croft et al. 2008; epidemiological modeling: May 2006; comparative analyses: Garland et al. 2005), and here we focus on the progress that has been made to date in identifying knowledge gaps where future research on bat-parasite dynamics could be focused.

Table 5.3 Summary of published articles using phylogenetically corrected comparative analyses to test the effects of species-specific socioecological traits on parasitism in bats

Number of bat species (families)	Location	Metric of parasitism	Social aspect	Analysis	Source
33 (7)	Southeast Asia	Viral richness, ecto- and endoparasite richness	Categorical metric of colony size and roost type	Phylogenetic least squares (PGLS) comparative analysis	1
33 (5)	Global	Viral richness	Colony size and population genetics (F_{ST})	PGLS comparative analysis	2
66 (8)	Global	Viral richness	Life-history traits: nonsignificant	PGLS comparative analysis	3
15 (6)	Africa	Viral richness	Colony size and roost type: nonsignificant	PGLS comparative analysis	4

[1] Gay et al. (2014), [2] Turmelle and Olival (2009), [3] Luis et al. (2013), [4] Maganga et al. (2014)

Table 5.4 Summary of published articles explicitly addressing links between microparasites and some aspect of host social behavior in bats

Species	Family	Location	Disease/Pathogen	Social aspect	Analysis	Ref
Myotis lucifugus, M. septentrionalis, M. sodalis, M. leibii, Perimyotis subflavus, Eptesicus fuscus	Vespertilionidae	North America	White-Nose Syndrome (WNS)	Effect of hibernation cluster size on WNS detection	Population surveys, statistical models	1
M. lucifugus, M. septentrionalis, M. sodalis, M. leibii, P. subflavus, E. fuscus	Vespertilionidae	North America	WNS	Variation in sociality between species	Population surveys, statistical models	2
M. lucifugus	Vespertilionidae	North America	WNS	Female philopatry and colony connectivity	Population Genetic Structure (F_{ST})	3
M. lucifugus	Vespertilionidae	North America	WNS	Effect of colony size on WNS risk	Population surveys, statistical models	4
M. lucifugus, M. septentrionalis, M. sodalis, M. leibii, P. subflavus, E. fuscus, M. emarginatus, M. myotis, M dasycneme, M. brandtii, M. mystacinus, M. daubentonii, M. nattereri, Pipistrellus pipistrellus, E. nilssonii, E. serotinus	Vespertilionidae	North America & Europe	WNS	Variation in pre- and post-WNS colony size of North American and European bat species	Population surveys and statistical models	5
E. fuscus	Vespertilionidae	USA	Rabies	Effect of colony size on rabies acquisition	Field data, statistical models	6

(continued)

Table 5.4 (continued)

Species	Family	Location	Disease/Pathogen	Social aspect	Analysis	Ref
E. fuscus	Vespertilionidae	Canada & USA	Hypothetical	Variation in fission–fusion dynamics between pregnant and lactating bats influences hypothetical pathogen dynamics	Social network analysis, epidemiological models	7
Nyctalus lasiopterus	Vespertilionidae	Spain	Hypothetical	Variation in roosting behavior and fission–fusion dynamics influences hypothetical pathogen dynamics	Social network analysis, epidemiological models	8
Desmodus rotundus	Phyllostomidae	Peru	Rabies	Effect of migration and group size on rabies prevalence	Field data, epidemiological models	9
D. rotundus	Phyllostomidae	Peru	Rabies	Effect of colony size on rabies seroprevalence	Field data, statistical models	10
M. myotis	Vespertilionidae	Germany	Coronaviruses, Astroviruses, and Adenoviruses	Effect of colony size on viral amplification	PCR to identify viruses, field data, and statistical models	11
Pteropus giganteus	Pteropodidae	Bangladesh	Nipah virus	Effect of roost selection and colony size on predicted Nipah outbreaks	Field data, epidemiological models	12
P. alecto, P. poliocephalus	Pteropodidae	Australia	Hendra virus	Colony size and absence of migratory behavior of urban populations	Field data, epidemiological models	13

(continued)

Table 5.4 (continued)

Species	Family	Location	Disease/Pathogen	Social aspect	Analysis	Ref
Eptesicus serotinus, Hypsugo savii, M. blythii, M.capaccinii, M. daubentonii, M. emarginatus, M. escalerai, M. myotis, Nyctalus leisleri, Plecotus auritus, P. austriacus, P. kuhlii, P. nathusii, P. pipistrellus, P. pygmaeus, Miniopterus schreibersii, Rhinolophus euryale, R. ferrumequinum, R. hipposideros, Tadarida teniotis	Vespertilionidae Miniopteridae Rhinolophidae Molossidae	Spain	European bat Lyssavirus	Effect of colony size on Lyssavirus seroprevalence	Field data, seroprevalence, and statistical models	14
Hypothetical	–	–	Hypothetical	Effects of fission–fusion dynamics, group size, and information exchange on predicted pathogen dynamics	Social network analysis, epidemiological models	15

[1] Langwig et al. (2012), [2] Langwig et al. (2015), [3] Miller-Butterworth et al. (2014), [4] Wilder et al. (2011), [5] Frick et al. (2015), [6] Pearce et al. (2007), [7] Webber et al. (2016), [8] Fortuna et al. (2009), [9] Blackwood et al. (2013), [10] Streicker et al. (2012), [11] Drexler et al. (2011), [12] Hahn et al. (2014), [13] Plowright et al. (2011), [14] Serra Cabo et al. (2013), [15] Kashima et al. (2013)

Table 5.5 Summary of published articles explicitly addressing the links between macroparasites and some aspect of host social behavior in bats

Species	Family	Location	Ectoparasite species	Social Aspect	Analysis	Ref
Myotis myotis, M. bechsteinii	Vespertilionidae	Switzerland, Italy, and Germany	*Spinturnix myoti,S. bechsteini*	Effect of host social system on parasite genetic structure	Field data, statistical analysis	1
Lophostoma silvicolum	Phyllostomidae	Panama	Streblid flies, Wing mites	Effect of mating and social systems	Review analysis	2
Noctilio albiventris, N. leporinus, Glossophaga soricina, Desmodus rotundus, Artibeus fimbriatus, A. jamaicensis, A. lituratus, Platyrrhinus lineatus, Pygoderma bilobatum, Sturnira lilium, Eptesicus fuscus, Lasiurus ega, M. albescens, M. nigricans, Eumops glaucinus, E. patagonicus, Molossops temminckii, Molossus ater, M. currentium, M. molossus, Nyctinomops laticaudatus	Noctilionidae Phyllostomidae Vespertilionidae Molossidae	Paraguay	*Noctiliostrebla maai, N. aitkeni, Paradyschiria parvula, P fusca, Ornithodoros hasei, Trichobius joblingi, T. parasiticus, Strebla weidemanni, Radfordiella desmodi, Periglischrus iheringi, P. ojasti, Macronyssoides kochi, M. conciliates, Paratrichobius longicrus, Aspidoptera falcata, Megistopoda proxima, Parichoronyssus euthysternum, Spinturnix surinamensis, Steatonyssus joaquimi, S. furmani, Macronyssus crosbyi, Hesperoctenes sp., H. parvulus, Chiroptonyssus haematophagus, C. venezolanus, C. robustipes, Parkosa maxima, P. tadarida*	Effect of sex-bias in host social system on ectoparasite abundance	Field data, statistical analysis	3

(continued)

Table 5.5 (continued)

Species	Family	Location	Ectoparasite species	Social Aspect	Analysis	Ref
Antrozous pallidus	Vespertilionidae	USA	*Steatonyssus antrozoi, Spinturnix orrii, Basilia antrozoi, Whartonia whartoni, Ornithodorus sp.*	Host roost switching and grouping behavior	Field data, statistical analysis	4
N. albiventris, N. leporinus, Glossophaga soricina, Carollia perspicillata, D. rotundus, A. fimbriatus A. jamaicensis, S. lilium, M. nigricans, M. molossus, M. rufus	Noctilionidae Phyllostomidae Vespertilionidae Molossidae	Paraguay	*Noctiliostrebla maai, N. aitkeni, N. dubia, Paradyschiria parvula, P. fusca, Xenotrichobius noctilionis, Strebla guajiro, S. weidemanni, Trichobius dugesii, T. uniformis, T. joblingi, T. parasiticus, T. jubatus Aspidoptera phyllostomatis, A. falcat,a Megistopoda aranea,.M proxima Metelasmus pseuodopterus, M. wenzeli, Basilia speiseri, B carteri, Hesperoctenes fumarius*	Effect of host aggregation and social structure on ectoparasite abundance	Field data, statistical analysis	5
M. bechsteinii	Vespertilionidae	Germany	*S. bechsteini*	Effect of host social system on ectoparasite population structure	Field data, genetic analysis, statistical analysis	6
M. bechsteinii	Vespertilionidae	Germany	*B. nana, S. bechsteini*	Effect of colony size and social system on ectoparasite abundance	Field data, statistical analysis	7

(continued)

Table 5.5 (continued)

Species	Family	Location	Ectoparasite species	Social Aspect	Analysis	Ref
M. bechsteinii	Vespertilionidae	Germany	*B. nana*	Effect of sociality and roost switching on ectoparasite reproductive success	Field data, statistical analysis	8
M. myotis, M. blythii, M. daubentonii, Plecotus auritus, Nyctalus noctula	Vespertilionidae	Switzerland	*S. andegavinus, S. myoti*	Host sex-bias in social system	Experimental trials, field data, and statistical analysis	9
Miniopterus schreibersii	Vespertilionidae	Portugal	*S. psi, S. myoti, Macronyssus granulosus, M. longimanus*	Host sex-bias in social system	Field data, statistical analysis	10
M. lucifugus	Vespertilionidae	Canada	*Myodopsylla insignis, S. americanus, M. crosbyi, Leptotrombidium myotis, Cimex sp.*	Host sex-bias in social aggregation	Field data, statistical analysis	11
M. myotis	Vespertilionidae	Poland	*S. myoti*	Effect of host colony size on ectoparasite abundance	Field data, statistical analysis	12
Tylonycteris pachypus, T. robustula	Vespertilionidae	China	*Macronyssus radovskyi*	Effect of host colony size on mite abundance	Field data, statistical analysis	13
Myotis daubentonii	Vespertilionidae	Czech Republic	*S. andegavinus*	Effect of host colony size and sex-bias in social aggregation	Field data, statistical analysis	14

(continued)

Table 5.5 (continued)

Species	Family	Location	Ectoparasite species	Social Aspect	Analysis	Ref
M. daubentonii	Vespertilionidae	Germany	*S. andegavinus*	Effect of host colony size on mite abundance	Field data, statistical analysis	15
M. bechsteinii	Vespertilionidae	Germany	*B. nana*	Effect of host roost selection on ectoparasite infestation	Experimental trials, field data, statistical analysis	16

[1] van Shaik et al. (2014), [2] Dechmann and Kerth (2008), [3] Presley and Willig (2008), [4] Lewis (1996), [5] Presley (2011), [6] Bruyndonckx et al. (2009), [7] Reckardt and Kerth (2009), [8] Reckardt and Kerth (2006), [9] Christe et al. (2007), [10] Lourenço and Palmeirim (2007), [11] Webber et al. (2015a), [12] Postawa and Szubert-Kruszynska (2014), [13] Zhang et al. (2010), [14] Luçan (2006), [15] Encarnaçao et al. (2012), [16] Reckardt and Kerth (2007)

5.2.1 Social Network Analysis

Social network analysis is based in mathematical graph theory and has been widely applied in human sociobiology, since the 1950s (e.g. Cartwright and Harary 1956; Wasserman and Faust 1994). For studies of wildlife, network analysis was first applied in primate sociobiology (e.g. Sade and Dow 1994), and has recently been applied more broadly to many other taxa (e.g. Fewell 2003; Hamede et al. 2009; Drewe 2010), including bats (for review see Johnson et al. 2013). Networks consist of nodes (individuals or locations) and edges (interactions between nodes) through which a variety of individual and group level metrics can be quantified (Wey et al. 2008). The roles and importance of individuals or locations can then be assessed based on these metrics (see Croft et al. 2008 for review). For example, individuals with certain combinations of traits can influence network dynamics by potentially acting as intermediaries connecting smaller subgroups within larger groups (Wey et al. 2008; Krause et al. 2010). In addition, bipartite networks (or two-mode networks) can be constructed to assess associations between individuals and ecologically relevant locations (e.g. a population of organisms and their nesting sites). Network metrics are especially useful because they can be used as predictor variables for relevant-dependent variables (e.g. infection status or parasite intensity) in standard statistical models (e.g. general linear models). Network analysis has allowed disease ecologists and parasitologists to make important strides quantifying how non-random social interactions affect parasite transmission and dynamics (for review see Godfrey 2013).

Network analyses have become increasingly popular for studies of bats (Johnson et al. 2013). For instance, network analyses have been applied in a bat-habitat management context by identifying critical roosting locations that serve as ‘hubs’ within a roost network and simulating the consequences of removing those key sites for stability of the social group (Rhodes et al. 2006; Silvis et al. 2014). Network analyses have also been used to identify and quantify fission–fusion behavior within bat colonies (Fortuna et al. 2009; Patriquin et al. 2010; Kerth et al. 2011; Johnson et al. 2012). In the context of disease ecology, so far only two studies have connected social networks with epidemiological models to make inferences about host–pathogen dynamics (e.g. Fortuna et al. 2009; Webber et al. 2016). Fortuna et al. (2009) showed that giant noctule bats (*Nyctalus lasiopterus*) form highly modular, fission–fusion colonies, and used an epidemiological model, parameterized using network metrics, to show that this arrangement reduces the spread of information or disease within the population because the colony was effectively segregated into modules divided among many roost trees (n = 73 trees for 25 bats: Fortuna et al. 2009). For big brown bats (*Eptesicus fuscus*), Webber et al. (2016) recently showed that network structure depends on the habitat context. Although tree-roosting *E. fuscus* reuse tree hollows between years (Willis et al. 2003), they frequently switch roosts within years (on average every 1.7 days: Willis and Brigham 2004) and rarely return to the same roost within a given summer. In building roosts, however, *E. fuscus* switch much less frequently and commonly return to the same roost repeatedly within the same year (Ellison et al. 2007; Webber et al. 2016). Webber et al. (2016) applied epidemiological models to social networks constructed based on these patterns of roosting behavior in forests versus buildings and found that parasite dynamics should vary between these habitat contexts with more rapid pathogen dissemination within building roosting colonies.

Constructing epidemiological models from empirical data undoubtedly improves inference for predicting epidemic outcomes, but as yet there are no studies that quantify real-world relationships between the social behavior of bat hosts and their parasites to test predictions of epidemiological models (Table 5.3). Although this form of data collection can be labor-intensive and potentially expensive (Craft and Caillaud 2011), there are numerous examples of network analysis being used to integrate information on host-contact patterns and parasitism in systems with highly gregarious hosts. For example, network analysis elucidated the role of meerkat (*Suricatta suricata*) allogrooming as a predictor for the prevalence of *Myobacterium tuberculosis*, the microparasite that causes tuberculosis (Drewe 2010). Quantifying association patterns of meerkats was largely conducted via focal animal observation, a type of data collection that is nearly impossible for free-ranging bats. Thus, advances in technology, such as passive transponders (PIT tags), data-logging telemetry, and/or proximity data loggers may be useful for quantifying association patterns and constructing social networks for bats with implications for epidemiology and disease ecology (e.g. Willis and Brigham 2004; Patriquin et al. 2010; Kerth et al. 2011; Johnson et al. 2012).

5.2.2 Epidemiological Modeling

Although empirical data are sparse, host-parasite dynamics, and the impacts of parasites on host populations have a rich theoretical history founded on Anderson and May's (1979) seminal models. Their classic microparasite epidemiological model conceptualizes host population dynamics in terms of susceptible (S), exposed (E), infected (I), and resistant/recovered (R) population pools, and these pools can be combined in a range of ways depending on the nature of host–pathogen interactions in the wild (e.g. SI, SIS, SIR, SEIR models). In a standard SIR model, individuals transition from S to I as a function of transmission rate (β) and from I to R as a function of survival of infection (v), while birth (a), and death rates (b, $a + b$ for infected hosts) of each pool drive overall population dynamics (Fig. 5.1; Anderson and May 1979). Since being developed, SIR epidemiological models have been widely used to infer microparasite impacts on host populations for humans (e.g. Anderson and May 1982), wildlife (e.g. McCallum et al. 2009) and plants (e.g. Gilligan et al. 1997).

Although appropriate for modeling the impacts of many infectious diseases (e.g. measles, whooping cough: Anderson and May 1992), classic SIR models compartmentalize individuals into broad categories which may fail to capture variation in aspects of host biology that could influence parasite dynamics and impacts (Keeling and Eames 2005). For example, classic SIR models often assume that individual hosts in the population associate at random but, particularly for highly social species, non-random association patterns are far more likely in nature. Incorporating network structure into epidemiological models eliminates random-mixing assumption of classic SIR models by assigning each individual a finite number of permanent or temporary contacts between which transmission can occur (Keeling and Eames 2005; May 2006). Implications for network epidemiological modeling include the ability to identify highly connected individuals that may be involved in a disproportionate number of transmission events (e.g. super-spreaders: Lloyd-Smith et al. 2005) and weakly connected individuals that may benefit from lower risk of infection. Epidemiological models informed by variation in social connectedness can be highly effective for predicting pathogen dynamics (Lloyd-Smith et al. 2005) but, as noted above, so far only two studies have applied these methods specifically to bats (Fortuna et al. 2009; Webber et al. 2016). However, to our knowledge no study has explicitly tested model predictions on a natural bat-parasite system in the wild.

An alternative to network epidemiological models informed by short-term (i.e. one season) association data, is the use of long-term population data for model parameterization. These data ideally include information on changes in population or colony sizes and changes in population demographic structure and/or vital rates. Most often for bats, long-term field data on colony size and population connectivity, in combination with laboratory data on immune physiology have been used (Table 5.4; George et al. 2011; Plowright et al. 2011). For example, field and laboratory data were combined to model ecological factors driving HeV spillover events occurring in Australia from flying foxes (*Pteropus* sp.) to horses and predicted that decreased migratory behavior of the host increased host density in urban areas, which contributed to the duration and intensity of HeV outbreaks (Plowright et al. 2011, see below). Similarly, mark-recapture data, combined with birth and death rates of different demographics, have been used to parameterize models of rabies dynamics (George et al. 2011). Rabies in *E. fuscus* is highly seasonal, with peaks in prevalence at maternity colonies (i.e. during June and July) after parturition when pups provide a supply of immunologically naive hosts (George et al. 2011). Thus, the chance of spillover is greatest during the post-parturition period when females roost in large colonies and the influx of juveniles in the population increases overall prevalence.

These studies highlight the value of predictive models incorporating the behavior of bats to make predictions about parasite dynamics, with potential implications for human public health. However, even models which incorporate host ecology and behavior (e.g. habitat selection) do not typically account for variation in social behavior which could also play an important role (Moore 2002). For microparasites, the two most likely parameters influenced by variation in social behavior are transmission rate (β) and the survival and subsequent reproduction of infected individuals (Fig. 5.1). For example, recent appreciation of individual differences in host behavior has led to the realization that homogenous mixing or so-called ‘mass action’ transmission may not reflect the dynamics of most host-parasite systems (McCallum et al. 2001; Moore 2002; Barber and Dingemanse 2010). Despite this realization, though, for many host–pathogen systems, estimating β can be difficult and modeling studies

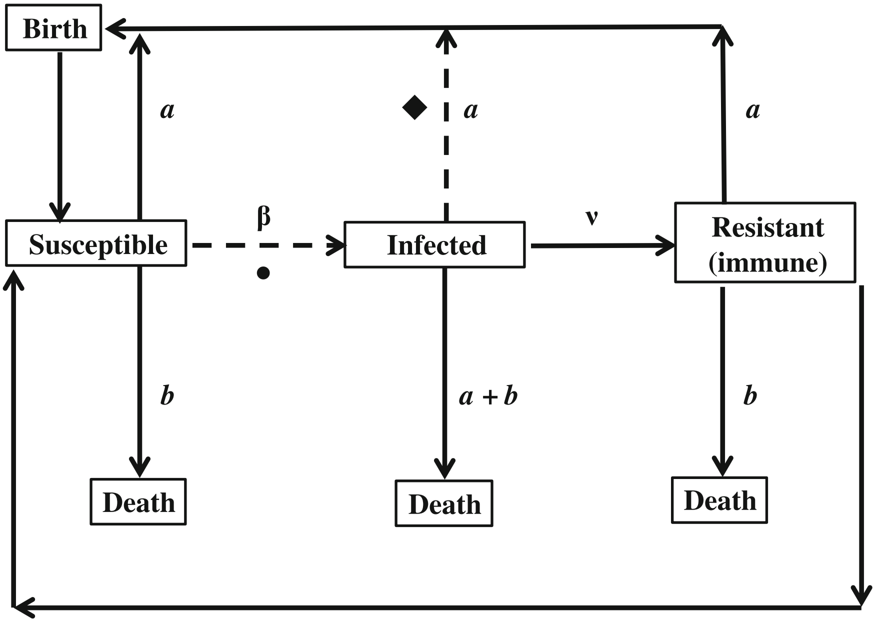

Fig. 5.1 Flow chart of the original compartment model of microparasite impacts on host populations based on population pools of susceptible, infected, resistant individuals (modified from Anderson and May 1979). Hosts shift from susceptible to infected as a function of transmission rate (β) and infected to resistant as a function of survival of infection (*v*), while birth (*a*) and death (*b*, *a* + *b* for infected hosts) rates drive population dynamics. Variation in host social behavior could impact β (•), which mediates the number of infected individuals as well as the subsequent fitness of infected individuals via reproductive rate (♦)

tend to rely on some plausible range of values for β (e.g. Griffin and Nunn 2012). For some microparasites, however, it may be possible to experimentally manipulate transmission and determine β empirically. For example, a basic pairwise experiment, where pairs of individuals (one infected, one susceptible) are housed together could help to determine the proportion of contacts that result in transmission, and narrow the range of plausible β values. Incorporating empirically derived data on association patterns of individual bats into epidemic models could help to improve our predictions of potential epidemic scenarios. These analyses (i.e. informed by empirical data) are still relatively scarce for bats (Table 5.4), but recent interest in host-parasite interactions and social network analysis provides an excellent opportunity to connect real data with model predictions.

5.2.3 Interspecific Comparative Analyses

Comparative analyses provide insight into potential species-specific variation in evolutionary adaption (i.e. changes in response to natural selection) within a group of organisms (Garland et al. 2005). From the perspective of parasites, a host is effectively a habitat, which means principles of community ecology, and biotic and abiotic characteristics of the "host ecosystem," can be used to explain patterns of parasite community composition (Morand and Poulin 1998). Thus, in contrast to intraspecific analyses which typically assess variation in prevalence or intensity of infection among individuals, comparative studies typically examine interspecific variation in parasite species richness among host species because intensity and prevalence are unlikely to be comparable in terms of their impacts, across different host and parasite species. In most cases, comparative studies of parasite species richness "correct for" host phylogeny. Two closely related species are more likely to share similar functional traits compared to two more distantly related species because of their more recent evolutionary history (Ives and Garland 2010). More parasites are also likely to have been identified for host species that have been well-studied so, in addition, most comparative studies also account for publication bias by including the total number of publications on a given host species as a covariate in statistical models, or by using residuals of a linear regression between number of publications and parasite species richness as the response variable (e.g. Nunn et al. 2003; Lindenfors et al. 2007; Turmelle and Olival 2009).

To date, relatively few studies have used comparative analyses to test effects of social behavior on parasite species richness in bats and, so far, most have focused on viruses with one quantifying macroparasites (Table 5.3). In contrast, studies of primates, the best-studied mammalian taxon in terms of relationships between social behavior and parasite richness, focus on a wider breadth of parasites (i.e. ecto and endoparasites as well as bacterial and viral pathogens: Nunn et al. 2003; Vitone et al. 2004; Griffin and Nunn 2012). For bats, colony size appears to be one of the most important predictors of viral richness, and epidemiological and evolutionary theory predict that highly colonial bat species should harbor greater parasite diversity, because of increased opportunities for parasite reproduction and evolution (Altizer et al. 2003). However, observed relationships have not always followed this pattern for bats (Turmelle and Olival 2009; Gay et al. 2014). Turmelle and Olival (2009) found no effect of colony size on viral richness in bats but, rather, identified species' conservation status and global F_{ST} (i.e. population genetic structure) as the most important predictors. On the other hand, among Southeast Asian bats, Gay et al. (2014) found a negative relationship between colony size and viral richness, which contradicts epidemiological theory (Loehle 1995). One potential limitation of these results could be that the authors used a categorical metric of population size (i.e. small, medium or large), which likely underrepresents the complexity of social behavior (Gay et al. 2014). Alternatively, in the case of Gay et al.'s (2014) results, it could be that bats in large colonies express immune or behavioral traits that provide protection from increased parasite risk in that social context.

Although they have still not been widely used, in our view comparative studies have great potential to help understand how bat social behavior influences parasite diversity and co-evolves with parasites, in part because bats are so diverse and exhibit a wide range of social and mating systems. For example, promiscuous bat species should host a greater number of parasite species compared to harem-breeding and monogamous bats because, independent of colony size or density, polygynandrous species presumably come in contact with a greater number of conspecifics during mating compared to polygynous species, which likely has implications for host-parasite coevolution. However, it is important to note that mating systems vary considerably among bats (McCracken and Wilkinson 2000) and other aspects of bat social systems (e.g. degree of fission-fusion or roost fidelity: see below) likely co-vary with mating system and are equally important as predictors of parasite richness. Thus, we recommend that future studies attempt to include more detailed information on bat social systems in comparative analyses. For example, a meta-analysis of primate social structure showed that differences in social network modularity (i.e. sub-grouping within a larger group) in 19 species led to differences in disease dynamics among species (Griffin and Nunn 2012). Although it may not be possible to include such detailed social association data for bats at present, as more social network studies accumulate, we recommend the use of network metrics as predictor variables of parasite richness in comparative analyses. Species-specific data on typical contact rates among individuals and demographics, and between sympatric species, as well as data on dispersal patterns and group stability within bat species (e.g. fission-fusion) would also be valuable as predictor variables to better understand how host social traits in bats influence their parasite ecology and evolution.

5.3 Examples from the Field: White-Nose Syndrome, Hendra Virus, and Arthropod Ectoparasites

Although very different in terms of their ecology and population impacts, based on our literature review, the relationship between bat sociality and parasite impacts and dynamics has been relatively well-studied for three sets of parasites: *P. destructans*, the cold-tolerant fungal pathogen of bats that causes WNS; HeV, which can lead to potentially fatal zoonotic disease in humans and horses; and the many species of arthropod ectoparasites which have been relatively well-studied because they can be easily sampled from bats captured in the field. We also identified four articles which addressed the relationship between rabies, or European Lyssavirus, and bat social behavior (Table 5.4), but rabies in bats has been the focus of a number of reviews (e.g. Messenger et al. 2003; Kuzmin and Rupprecht 2006; Rupprecht et al. 2011; O'Shea et al. 2011) so here we focus on less well-characterized bat-parasite interactions.

5.3.1 Host Sociality and Phenology in Bat WNS

WNS is an EID of urgent conservation concern because it is causing staggering rates of mortality among hibernating bats in eastern North America (Blehert et al. 2009; Frick et al. 2010; Wilder et al. 2011; Langwig et al. 2012; Frick et al. 2015).

Despite its recent emergence (2006–07), however, WNS is among the most well-studied microparasites of bats in the context of social behavior. Interestingly, one of the hallmark behaviors observed for *P. destructans* infected bats, both in the wild and in the laboratory, is a reduction in clustering behavior as WNS infection progresses over the course of hibernation (Langwig et al. 2012; Wilcox et al. 2014). This phenomenon could lead to increased energy expenditure or evaporative water loss which has implications for survival and potentially future reproduction (Willis et al. 2011; Boratyński et al. 2015). Reduced clustering could be part of a stereotyped behavioral response by animals to infection, known as "sickness behavior" (Hart 1988), which could either reduce the likelihood of becoming infected, or reinfected, by sick individuals in the hibernaculum or reduce the likelihood of infecting susceptible individuals, which could be important for inclusive fitness if bats cluster with kin during hibernation (Wilcox et al. 2014; Bohn et al., in review). In the laboratory, transmission occurs via direct physical contact and there is no evidence of airborne transmission (Lorch et al. 2011), while environmental transmission in the wild likely contributes strongly to infection dynamics because *P. destructans* can survive in hibernacula in the absence of bats (Verant et al. 2012; Hoyt et al. 2015). Although the most adversely affected bat species tend to associate with large numbers of conspecifics throughout the year, transmission appears to occur almost exclusively within hibernacula during autumn and throughout the winter (Langwig et al. 2015).

Variation in sociality within and between bat species appears to influence host-parasite dynamics in WNS. In the context of host density, there are two theories relevant to the relationship between transmission and host-parasite dynamics. First, density-dependent transmission predicts that host infection scales as a function of host density so that, at low host density, pathogen transmission declines, and a given pathogen fades out (Greer et al. 2008). Second, frequency-dependent transmission predicts that host infection is driven by the total number of interactions among infected and susceptible individuals in the population, regardless of population density, so that when host density is low, a given pathogen can persist (Greer et al. 2008). Interestingly, the relationship between WNS transmission and host density during hibernation appears to be species-specific. Among relatively solitary species (i.e. *Perimyotis subflavus* and *Myotis septentrionalis*) that hibernate individually or in small clusters, aggregation size (i.e. the numbers of bats in the hibernaculum) best predicted the number of surviving bats within a given hibernaculum, with larger aggregations experiencing faster apparent declines (Langwig et al. 2012). This observation is consistent with density-dependent transmission models. In contrast, for species that vary more widely in aggregation size (i.e. *M. lucifugus* and *M. sodalis*), mortality was equally severe across a range of aggregation sizes (Langwig et al. 2012), which is consistent with frequency-dependent transmission models. This suggests that differences in species-specific social behavior during hibernation can modulate WNS transmission and infection.

Unlike other infectious diseases of bats (e.g. rabies: George et al. 2011) demographic structure in the active season does not appear to drive WNS dynamics. Healthy *M. lucifugus* emerge from hibernation over an approximately eight-week period in spring (Norquay and Willis 2014; Czenze and Willis 2015). Females tend to emerge prior to males, with the females in the best condition emerging first. This is presumably because larger fat reserves allow females to cope with potentially inclement weather, but also initiate reproduction earlier by exploiting warmer, passively heated maternity roosts, and occasional warm nights with flying insects available (Norquay and Willis 2014). However, bats infected with *P. destructans* tend to emerge from hibernation much earlier than healthy bats presumably because their fat stores are depleted. Moreover, bats that survive hibernation with WNS often have severe wing damage in spring and individuals with the most damaged wings tend to have the smallest energy reserves (Fuller et al. 2011). For many diseases, an influx of immunologically naive hosts (i.e. juveniles) leads to a dramatic increase in prevalence immediately following reproduction due to vertical transmission from mothers to offspring. In WNS, however, seasonal dynamics of the disease are driven by dramatic seasonal changes in host physiology, specifically sustained low body temperature during hibernation (Warnecke et al. 2012; Langwig et al. 2012, 2015). For *P. destructans*-infected bats in spring and early summer, an increase in body temperature limits infection and transmission despite the fact that females tend to aggregate in potentially large maternity colonies (Langwig et al. 2015).

Although transmission likely does not occur readily for females at maternity colonies, high mortality rates during hibernation may decrease the number of potentially reproductive females that form maternity colonies (Langwig et al. 2015). Therefore, normal benefits incurred from colonial roosting, such as social thermoregulation, may be dramatically reduced for WNS-surviving bats, which could have additional negative impacts on survivors. For example, the energetic costs of wound healing may be significant for infected individuals upon emergence from hibernation (Fuller et al. 2011) and the decreased availability of social thermoregulation and increased likelihood of roosting solitarily may further increase energetic expenditure (Wilcox and Willis 2016). Therefore, for species affected by WNS, the lack of potential colony members, and thus potential for social thermoregulation, during spring and early summer could ultimately result in decreased survival and reproduction (Langwig et al. 2015).

In addition to influencing transmission of *P. destructans*, theory predicts that population size influences risk of extinction (de Castro and Bolker 2005). Using counts of bats during winter hibernaculum surveys as a proxy for population size, Frick et al. (2015) showed that, for five of six WNS-affected species, probability of local extinction from a given hibernaculum decreased as population size increased. This suggests that host aggregation and social behavior could influence risk of extinction from WNS. One possible mechanism is that larger populations have greater flexibility to cope with decreases in population numbers, and are thus less likely to face declines below population thresholds where extinction becomes inevitable.

Interestingly, social behavior may also help to explain differences in the consequences of *P. destructans* infection for European versus North American bats. Prior to the emergence of WNS, hibernating aggregations of affected North

American species were approximately tenfold higher, on average, than colony sizes of ecologically similar European species (Frick et al. 2015). However, after WNS emergence, colonies of affected North American species have declined precipitously and appear to be stabilizing at sizes similar to those of European bats (Frick et al. 2015). This suggests the possibility that European colony sizes could have been larger in the past and similar to pre-WNS colony sizes in North America (Frick et al. 2016). Taken together, empirical data from North America and inferences from Europe suggest that WNS could select against larger colony sizes (Frick et al. 2016) resulting in remnant colonies which are, on average, smaller and less social than pre-WNS colonies. We suggest that future studies attempt to quantify social tendencies at the individual and population levels for pre- and post-WNS infected populations to assess the impact of this conservation pathogen for social evolution in bats.

5.3.2 Anthropogenic Changes to Flying Fox Socioecology: Implications for HeV

In Australia, bats from the genus *Pteropus* are reservoir hosts for HeV, a recently emerged zoonotic virus from the family *Paramyxoviridae*. Flying foxes are only briefly infectious with no clinical disease but shed HeV in urine, saliva, feces, and placental fluids (Halpin et al. 2011). HeV is lethal to horses and humans, and transmission presumably occurs when horses ingest food or water contaminated by bats (Plowright et al. 2008). Horses appear to act as amplifier hosts (Daszak et al. 2006), as all human cases have been directly traced back to an infected horse (Field et al. 2012). Although, spillover events from flying foxes to horses are complex and few data exist linking individual social tendencies of the bats to HeV transmission, host socioecology likely mediates host–pathogen dynamics for this zoonotic disease.

Colony/aggregation sizes of *Pteropus* species can range from as few as 10,000 individuals in *P. alecto* maternity colonies to millions of individuals for *P. scapulatus*. Based on experimental data and closely related human paramyxoviruses (e.g. measles), HeV may require large host population sizes to provide enough susceptible individuals for persistence because of a relatively short infectious phase and life-long host immunity (Daszak et al. 2006). Historically, naturally occurring nectar resources in native forests supported large, seasonally-migrating flying fox populations (Eby 1991; Plowright et al. 2015) but human-mediated habitat alterations have resulted in patchily distributed natural food resources, which were already ephemeral in nature (i.e. seasonally produced nectar). Therefore, flying foxes have begun to colonize urban and periurban areas to exploit highly abundant, consistently available anthropogenic food resources, such as fruiting trees planted in gardens or horse paddocks (Eby et al. 1999). In many cases, urban bats do not migrate because food resources are consistently available, which increases the likelihood of HeV-positive bats coming in contact with horses (Plowright et al. 2011). Therefore, recent emergence and spillover of HeV in Australia appears directly linked to increases in the size and abundance of urban bat colonies as well as reduced migratory behavior (Plowright et al. 2015). Although urban bat aggregations appear to remain relatively large throughout the year, temporal dynamics of HeV are at least partially mediated by host socioecological traits such as colony size and migration (Plowright et al. 2011).

5.3.3 *Host Colony Size and Arthropod Ectoparasites in Female Temperate Bats*

As noted above, social group size has been identified as a potentially important predictor of parasitism, with larger groups generally hosting more parasites (Côté and Poulin 1995; Rifkin et al. 2012; Patterson and Ruckstuhl 2013). Among temperate bats, sexual segregation and variation in social group size between sexes appears to be among the most important mediators of ectoparasitism. Adult males tend to roost individually or in small groups, while females form maternity colonies (Kunz and Lumsden 2003). For males, parasitism tends to remain low-throughout spring and early summer and as the mating season progresses ectoparasite prevalence and intensity increases (Webber et al. 2015a). Most studies investigating the link between colony size and ectoparasitism in bats have found the predicted positive relationship (e.g. Luçan 2006; Reckardt and Kerth 2009; Encarnaçao et al. 2012), although this is not always the case (e.g. Zhang et al. 2010; Postawa and Szubert-Kruszynska 2014). One explanation for lack of correlation between group size and ectoparasitism at female colonies in some studies may be linked to variation in host association patterns and roost selection/ephemerality. For instance, bamboo shoots used as roosts by flat-headed bats (*Tylonycteris pachypus* and *T. robustula*) are highly ephemeral and likely contribute to frequent roost-switching (Lewis 1995) as well as variation in group size and composition (Zhang et al. 2010). Frequent roost switching breaks up social contacts that could favor direct host–host transmission of ectoparasites. Meanwhile, because some ectoparasites rely on stable roost structures for a portion of their reproductive cycles, bats that use ephemeral roosts rarely come in contact with ectoparasites that rely on a stable roost for reproduction (Lewis 1995), which could supersede the theoretical relationship between colony size and parasite risk.

Although, social contacts among females help to explain observed patterns of ectoparasitism at maternity colonies, social organization (i.e. composition of groups) can also mediate ectoparasitism. Most females present at maternity colonies are either pregnant or lactating and links between temporal variation in social organization (i.e. transition from pregnancy to lactation) and ectoparasitism are supported by co-evolution of some host-ectoparasite reproductive cycles (Christe et al. 2000). For example, reproductive cycles of some mite species respond to pregnancy hormones of their female hosts (Lourenço and Palmeirim 2007). Once pups are born there is also a pulse of mites, which results in significant vertical transmission from adult females to juveniles (Christe et al. 2000; Luçan 2006). Lactating females may also tolerate significant ectoparasite burdens. During lactation, females may have less energy available to mount behavioral (i.e. grooming) or immunological responses to infection (Zuk and McKean 1996; Christe et al. 2000). Thus, while females are lactating and pups are non-volant, ectoparasite prevalence, and intensity can be exceptionally high. However, once pups have been weaned and are volant, they tend to be more heavily parasitized than females until the colony disperses because they presumably have a naive immunoresponse and less-experience grooming (Christie et al. 2000; Czenze and Broders 2011). Although ectoparasitism tends to increase with colony size, juveniles are usually the most infected hosts at maternity colonies. Adult females still face significant ectoparasite burdens, while ectoparasitism for adult males generally increases throughout swarming as conspecific contact rates increase (Webber et al. 2015a).

Many bat ectoparasites are also vectors for bacterial pathogens (e.g. *Bartonella* sp., Veikkolainen et al. 2014). Transmission of bacterial or viral pathogens via ectoparasite vectors among bat hosts could be influenced by sociality, especially for highly gregarious females at maternity colonies. In theory, the same principles which regulate host–pathogen dynamics should also apply to host–vector–pathogen dynamics, where the duration and frequency of host-host contact facilitates ectoparasite transmission, which in turn facilitates vector-based pathogen transmission. For instance, recent empirical evidence suggests that wing mites (*Spinturnix* sp.) can transmit *P. destructans* propagules among hibernating bats in Europe, a chain of transmission which is facilitated by direct host-host contact (Luçan et al. 2016). We suggest that more future studies quantify links between host sociality, vector ectoparasites, and vector-borne bacterial, viral, and fungal pathogens.

5.4 Future Directions and Testable Hypotheses

Progress has been made in identifying relationships between some aspects of sociality and parasitism in bats, but much more empirical data from wild and captive bats of more species is certainly needed. We propose a series of testable hypotheses and possible experimental and observational studies about the role of bat sociality in parasite dynamics. We focus on two aspects of sociality which have been relatively little-studied for bats in the context of parasitism: fission–fusion dynamics and consistent individual differences in behavior or personality.

5.4.1 Fission-Fusion Dynamics

Fission–fusion is the temporary splitting and reforming of colonies, where lack of consensus, or even conflict, result in temporary fission, but the cost of remaining apart is greater than subsequent fusion (Sueur et al. 2011). Within maternity colonies, females exhibit fission–fusion sociality (e.g. *M. bechsteinii*: Kerth and König 1999; *Nyctalus lasiopterus:* Popa-Lisseanu et al. 2008) and change roosts every few days but not all members of the group will move together, resulting in variable group size and composition (e.g. Patriquin et al. 2010). Fission–fusion sociality and frequent roost switching by forest-living bats may have evolved as a mechanism to avoid parasites (Reckardt and Kerth 2007; Bartonička and Gaisler 2007), although a trade-off between the costs of parasitism and benefits of remaining loyal to high-quality roosts likely exists. Empirical data have linked fission–fusion behavior to ectoparasite avoidance (e.g. Reckardt and Kerth 2007) and some theoretical modeling also supports this hypothesis (Kashima et al. 2013). However, there are currently no studies investigating microparasite transmission within fission–fusion societies. We hypothesize that the relationship between fission–fusion dynamics and parasite risk and impacts will vary depending on the mode of transmission for a given type of parasite. We expect that for most microparasites and some ectoparasites (e.g. *Basilia nana*: Reckardt and Kerth 2007) that require direct contact between hosts for transmission, fission–fusion dynamics could serve to disrupt parasite transmission. Bats that display fission–fusion behavior typically switch roosts every 1–2 days (Willis and Brigham 2004) and data from *M. bechsteinii* suggest that bats are able to detect roosts that have recently been occupied by other bats (Reckardt and Kerth 2007). Thus, when bats switch roosts they appear to select sites that have not been occupied recently which could help them avoid infested roosts. In contrast, we expect that for macroparasites with alternative transmission strategies, such as mobile ectoparasites (e.g. crawling or flying), fission–fusion dynamics are likely to be less effective as a parasite-avoidance strategy. In fact, theory predicts that bats would be more likely to avoid mobile ectoparasites if they remained in a single, large group because of encounter-dilution effects (Côté and Poulin 1995; Rifkin et al. 2012). We suggest studies employing social network analysis of wild bats, combined with estimates of micro- and macroparasite prevalence, and intensity to disentangle relationships between host social behavior, including fission–fusion dynamics, and the ecology of parasite transmission (for review see Godfrey 2013).

5.4.2 Consistent Individual Differences in Behavior

Animal personality refers to consistent individual differences in behavior that are stable within an individual across time and situations (Sih et al. 2004; Wolf and Weissing 2012). Recently, personality has become more widely appreciated as a possible explanatory variable for a number of ecologically relevant traits including juvenile development (Stamps and Groothuis 2010), energy expenditure (Careau et al. 2008) and social structure (Krause et al. 2010; Wolf and Krause 2014). Because personality influences non-random association patterns observed within social groups (Krause et al. 2010), between-individual variation in personality traits are expected to influence parasite transmission patterns within and between groups

(Barber and Dingemanse 2010; Kortet et al. 2010). In general, the most active, exploratory or sociable (see Table 5.2 for definitions) individuals are expected to face greater risk of transmitting and/or acquiring parasites (Barber and Dingemanse 2010; Kortet et al. 2010). Despite enormous recent interest in animal personality among behavioral ecologists, evolutionary physiologists, and conservationists (for review see Sih et al. 2004; Réale et al. 2007; Careau et al. 2008; Wolf and Weissing 2012), there are currently only three published studies examining effects of personality on any ecological trait in bats (Menzies et al. 2013; Kilgour and Brigham 2013; Webber et al. 2015b). These studies highlight that individual bats, like many other vertebrates exhibit differences in personality but there is clearly room for much more research on personality in bats, especially in the context of parasite dynamics.

We propose a series of hypotheses that would help to understand relationships between personality and parasite prevalence/intensity and transmission in the context of sociality. As for the implications of fission–fusion dynamics described above, these hypotheses vary for contact-mediated micro- and macroparasites versus mobile macroparasites with host-seeking behavior. First, we hypothesize a relationship between individual sociability and parasitism for contact-mediated parasites. Theory predicts a positive relationship between host sociability and parasite risk, because the most sociable individuals are the most highly connected group-members within the social network and may therefore be exposed to, and themselves transmit, a disproportionate number of infections (Barber and Dingemanse 2010). By contrast, for parasites with active host-seeking behavior, individual activity and exploration may be most important because less active or exploratory individuals may be easier targets for mobile macroparasites. Webber et al. (2015b) identified the expected negative relationship between the prevalence and intensity of fleas (a relatively mobile ectoparasite) and the activity component of personality for female, but not male *M. lucifugus*, which highlights the potential complexity of these relationships. Personality may have had a larger effect on females because females may be selective with their mating partners, so if less active females mate with fewer males they may retain a higher proportion of fleas, which would otherwise be transmitted during mating (Webber et al. 2015b). We suggest that future studies attempt to disentangle relationships between contact versus mobile parasites and sociability, activity, and exploration components of personality in bats.

5.5 Conclusion

Studies of host-parasite dynamics in bats are important from both a conservation and human public health perspective and, as we describe above, the implications of bat social behavior for parasite risk can be dramatic. Based on our review of the literature, we identified social network analysis, epidemiological modeling (often, though not always, parameterized using empirically-derived data), and phylogenetically-informed comparative analyses as the methods most commonly used for quantifying links between sociality and parasitism in bats. In general, these studies suggest complex relationships and studies aimed at fully elucidating these links may require integration of techniques and data collection from multiple disciplines (e.g. behavior, ecology, epidemiology, parasitology, and physiology/immunology).

We also found that, despite its recent emergence, WNS is already among the best-studied pathogens of bats in the context of sociality perhaps, in part because researchers who focus on bats have brought behavioral and ecological expertise to bear on this important conservation problem. The link between host social aggregation and HeV is also well established, again likely because of perceived societal importance, in this case due to the public health implications of a zoonotic pathogen. Relationships between bats and their ectoparasites have also been relatively well studied, perhaps partly because ectoparasites are relatively easy to quantify when bats are in the hand. Ectoparasite studies have identified links between parasite risk, colony size, and fission–fusion dynamics which have broad implications for understanding how sociality affects host–parasite interactions in bats. A few studies have also begun to understand bats in the context of individual animal personality. In general, however, we advocate for more research on bat parasites in the context of socioecology, especially for bat and parasite species which have received little attention to date.

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Part II

Information Transfer to Communicate Bat Facts

Chapter 6
The Complex Songs of Two Molossid Species

Kirsten Bohn, Fernando Montiel-Reyes and Israel Salazar

Abstract Birds are well known for songs while bats are well known for their developed sonar system. The chiropteran echolocation system has a long and extensive history of research because of the highly specialized neurocircuitry required for vocal production, perception, and vocal-motor integration. However, recent research has revealed that in addition to echolocation, bats produce highly sophisticated social vocalizations whose complexity is only rivaled by birds, humans, and cetaceans. In this chapter we discuss and define the terms "song" and "courtship call", outline how acoustic signals are analyzed, and review what families of bats produce songs and calls. We then compare behavior, song structure, individual variation, and regional dialects in two species of Molossids, *Tadarida brasiliensis* and *Nyctinomops laticaudatus*. *T. brasiliensis* is a bat that sings like a bird—they produce songs with three key songbird features: hierarchical structure, syntactical organization, and syntactical flexibility. *T. brasiliensis* songs are composed of four main syllable types: *chirp A* ("*A*"), *chirp B* ("*B*"), *trill* and *buzz*. Syllables are combined to form three phrases, *chirp*, *trill*, and *buzz* and phrases are then combined to form songs (hierarchical structure). Specific syntactical rules are followed for combining phrases (syntactical organization). However, the number of syllables within a phrase and the number and order of phrases vary from one rendition to the next (syntactical flexibility). *N. laticaudatus* produce the same types

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of syllables and phrases as *T. brasiliensis*. However, the spectro-temporal structure of A and B syllables of *N. laticaudatus* are quite different, and they show much lower syntactical flexibility in combining phrases. Finally, while *T. brasiliensis* males produce highly stereotyped chirp syllables that do not vary between regions, *N. laticaudatus* chirp syllables are not stereotyped within males but do vary across regions. These findings are the first to show that complex songs are not only produced by a single bat species and that many aspects of songs are highly conserved across species.

6.1 What are Songs?

Functionally, "songs" are acoustic courtship displays. They are sexually selected signals produced predominantly by males during mating seasons for mate attraction and male-male competition (Bradbury and Vehrencamp 1998; Simmons et al. 2003). As such, the main evolutionary forces for song production and structure are female preference and intrasexual competition. Acoustic displays that serve courtship functions are nearly ubiquitous across animals, including cricket "songs", cicada calls, deer roars, and frog calls, just to name a few. Although the function of courtship displays may be common across many taxa, the complexity of acoustic courtship displays varies greatly.

Structurally, the term "song" has been reserved for more complex courtship vocalizations whereas the term "call" has been used for simpler vocalizations (e.g., "courtship calls" or "advertisement calls"). This originates from the complexity of birdsong produced by Passeriformes. These songs are longer and contain multiple types of elements (e.g., syllables, notes, and/or phrases) that are often combined in a stereotypical manner with regular temporal structure (Catchpole and Slater 2008; Collins 2004; Marler and Slabbekoorn 2004). Calls on the other hand are formed from single elements (notes or syllables) or simple repetitions of one or a few elements. Another major difference between mating "calls" and "songs" is that song element patterns are highly structured, with individual, regional, and/or species-specific patterns (Balaban 1988; Becker 1982; Catchpole and Slater 2008). Finally, at the most complex level, birdsongs are often hierarchically organized where notes are combined into syllables, syllables into motifs and motifs into phrases with multiple layers of repetition or periodicities (Catchpole and Slater 2008; Collins 2004; Marler and Slabbekoorn 2004). Although this complexity does not modify the function of songs, it does require specializations for vocal production that parallel human speech (Marler 2004). In addition to songbirds, complex, hierarchically structured vocalizations have only been found in cetaceans (Payne and McVay 1971), hyraxes (Kershenbaum et al. 2012) and bats (Bohn et al. 2009). Here we will create a definition of song and call based on songbird research and the types of courtship vocalizations that have been observed in bats. First, however, we will provide a primer on acoustic signals.

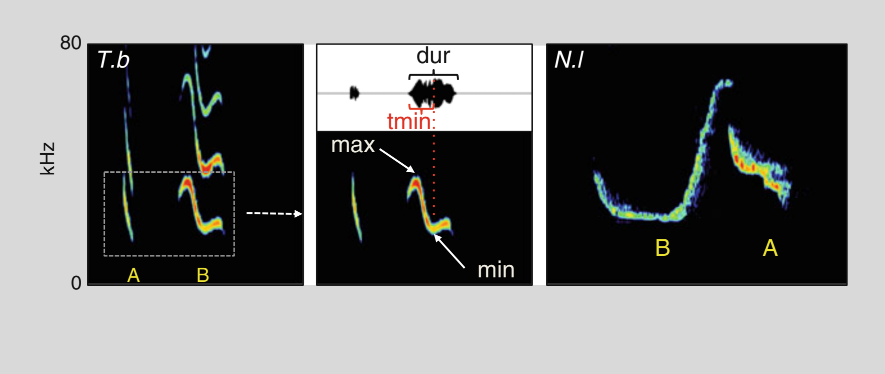
Complex acoustic signal features can be broadly grouped into three categories: element acoustics, temporal patterning, and syntax (Box 1). Element acoustics are measurements of individual elements, which we refer to as “syllables” but are also known as “notes” in song or “pulses” in echolocation. These measurements include temporal features (i.e., duration), spectral features (i.e, peak frequency), and spectro-temporal features. Spectro-temporal features can be thought of as the “shape” of a signal, that is, the change in frequency over time. Temporal patterning includes repetition rates of elements within phrases and periodicity. Finally, syntax is the way in which elements are ordered and combined as has commonly been used in birdsong (Balaban 1988; Kroodsma et al. 1982) and the term does not address the “meaning” of vocalizations in any way. Syntactical features include the number, type and order of phrases in songs (i.e., “songtype”, see Fig. 6.2).

Box 1—Measuring and describing songs

The two main types of features measured in acoustic communication. Element acoustics include temporal, spectral (frequency), and spectro-temporal (changes in frequency over time) measurements of individual elements, i.e., “syllables” or “notes”.

Feature type	Examples
Element acoustics	
Temporal	Duration (*dur*)
Spectral	Maximum (*fmax*), Minimum (*fmin*)
Spectro-temporal	Location minimum (*lmin* = *tmin/dur*)
	Location maximum (*lmax* = *tmax/dur*)
Syntax	
Phrase level	Number of elements
	Relative number of different elements
Song level	Phrase order = *song type*
	Number of phrases

Acoustic measurements of chirp A and chirp B syllables of *T. brasiliensis* (*T.b*) and (*N.l*). The far left panel shows an entire A and B syllable with harmonics. For measurements only the fundamental frequency was used (middle and right panels).



Songs—Composed of at least three types of syllables (that is more than just two alternating syllables) and either have (a) specific combinatorial but variable element content and order (i.e, song types) (b) hierarchical structure, or (c) have many syllables (for example *S. bilineata* with estimates of more than 80 syllable types (Davidson and Wilkinson 2002).

Calls—Calls are predominantly composed of single syllables produced in trains. However, in cases with multiple syllable types they do not have variable syntax or hierarchical structure.

6.2 Bat Courtship Vocalizations

Courtship vocalizations with observed behaviors have been documented in eight families (Fig. 6.1 and Table 6.1). This likely greatly underestimates the number of species that use vocal displays in courtship. In fact, vocal displays should be highly common, if not ubiquitous, since bats live in low light environments that often preclude the use of visual signals and have a specialized audio–vocal system for echolocation. Unfortunately observing mating or any behaviors in typical bat roosts like inside caves, crevices or trees is especially difficult.

Only two species of bats outside of Molossidae have been documented producing songs (Table 6.1). The first, *Saccopteryx bilineata* is, so far, most well-studied because it roosts out in the open on trees during the day. Songs are used in association with courtship displays and defense of roosting territories where female harems reside (Behr and von Helversen 2004; Bradbury and Emmons 1974; Bradbury and Vehrencamp 1977). Song production rates and acoustic features affect mating success and indicate male quality (Behr et al. 2006). There is no evidence yet of hierarchical structure or specific syntax in *S. bilineata* songs but they are complex in content with individual males can produce up to 80 different syllables whose use varies across renditions (Davidson and Wilkinson 2002). The Vespertilionid, *Pipistrellus nathusii* is the second species of bat that produces song. They too have a harem structure but males not only sing at roost entrances but also

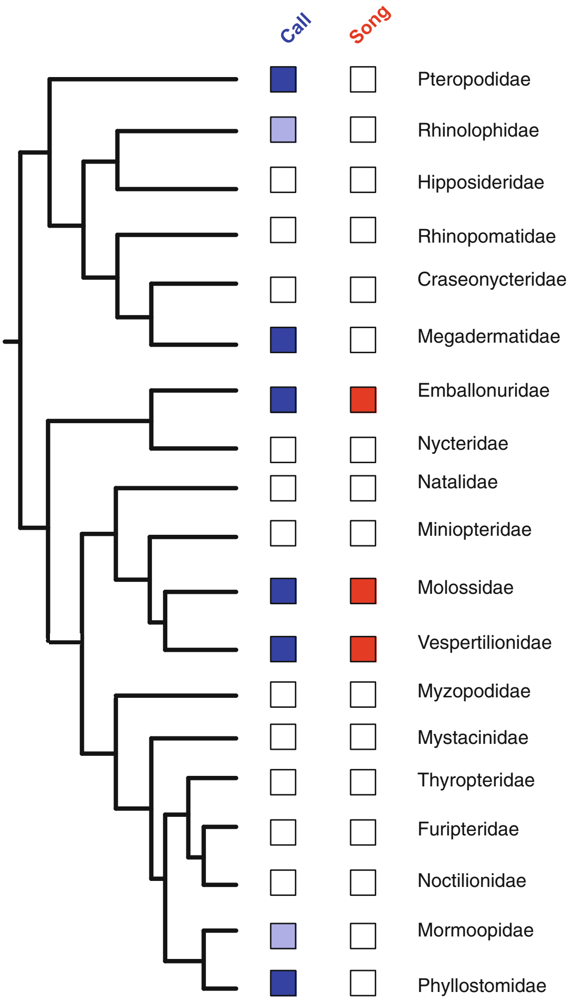


Fig. 6.1 Phylogeny of bat families adapted from Teeling et al. (2005) with color coded boxes for whether bats in the family produce simple courtship/advertisement calls (*blue*) or songs (*red*). The *light blue* boxes are for species that have extensive vocal repertoires and are thought to produce courtship calls but have not been directly observed calling in mating contexts

in flight (Jahelková et al. 2008). *P. nathusii* songs are hierarchically organized with syllables combined into phrases (termed motifs) and phrases combined to form songs (Jahelková et al. 2008). Data suggest that each phrase carries different information and so different phrase combinations result in different complex messages (Jahelková et al. 2008).

Our current information on courtship vocalizations, albeit quite limited, has strong implications. First, there is a wide range in vocal complexity in courtship signals across taxa. Second, the bat species that do produce songs are from families that have species that also produce simple calls. Thus, complex song has likely evolved at least three times in bats. These findings make bats an exciting model for comparative research on the evolution of vocal complexity.

Table 6.1 Species that have been shown to produce courtship/advertisement calls or song

Family	Song/call	Species	Notes and references
Rhinolophidae	Call (likely)	*Rhinolophus ferrumequinum*	Produce lots of social calls of varying complexity (Andrews and Andrews 2003; Ma et al. 2006)
Mormoopidae	Call (likely)	*Pteronotus parnellii*	Produce lots of social calls of varying complexity (Clement and Kanwal 2012; Kanwal et al. 1994)
Pteropodidae	Call	*Pteropus poliocephalus* *Hypsignathus monstrosus*	Bradbury (1977), Nelson (1964)
Megadermatidae	Call	*Cardioderma cor* *Megaderma lyra* *Lavia frons*	Leippert (1994), Vaughan (1976), Vaughan and Vaughan (1986)
Phyllostomidae	Call	*Carollia perspicillata* *Erophylla sezekorni*	Knörnschild et al. (2014), Murray and Fleming (2008), Porter 1979)
Emballonuridae	Call, song	*Coleura seychellensis* (call) *Saccopteryx bilineata* (song)	Behr and von Helversen (2004), Davidson and Wilkinson (2002), Gerlach (2009)
Molossidae	Call, song	*Molossus molossus* (call) *M. rufus* (call) *T. brasiliensis* (song) *N. laticaudatus* (song)	Bohn et al. (2008), Bohn (pers. observ.)
Vespertilionidae	Call, song	*Neoromicia. nanus* (call) *Pipistrellus pipistrellus* (call) *Nyctalus nyctalus* (song) *P. nathusii* (song) At least six other species with courtship/advertisement calls.	Barlow and Jones (1997), Jahelková et al. (2008), Lundberg and Gerell (1986), O'Shea (1980), Pfalzer and Kusch (2003)

In this chapter we will examine and compare the songs of two Molossid species, *Tadarida brasiliensis,* and *Nyctinomops laticaudatus* (Fig. 6.2). First we discuss individual and regional variation in vocalizations as these have been studied in such great depth across species. We then describe the behaviors and songs produced by *T. brasiliensis* and use those observations to test whether *N. laticaudatus* vocalizations function as songs since they are extremely difficult to directly observe in their roosts (wall cracks). We then compare song syntax between the two species and examine individual and regional variation in the two species' chirp syllables.

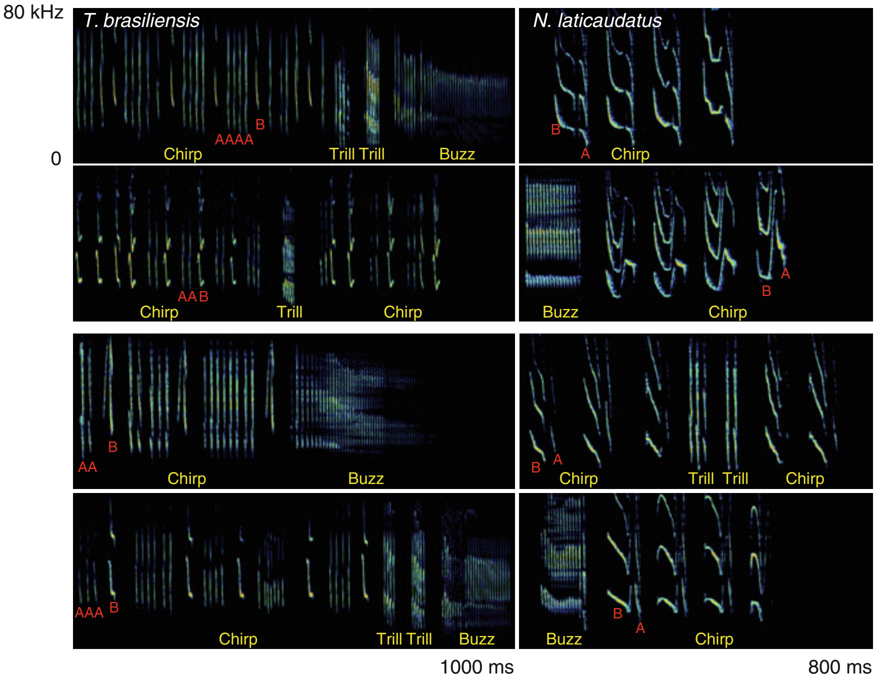


Fig. 6.2 Songs of *T. brasiliensis* (*left*) and *N. laticaudatus* (*right*). *Yellow labels* are phrases (chirp, trill, buzz), *red labels* are for Chirp Type A and Chirp Type B syllables. Each song is from a different animal. The *top* two songs of *T. brasiliensis* are from Austin, Texas, and the *bottom* two songs are from College Station, Texas. Each song can be described as a song type. The song types of the *top* two songs of *T. brasiliensis* from *top* to *bottom* are *chirp-trill-buzz* and *chirp-trill-chirp*. The *top* two songs of *N. laticaudatus* are from Antigua, Mexico and the *bottom* two songs are from Uxmal, Mexico. All songs (both species) are on the same frequency and temporal scales

6.3 Individual and Regional Variation

Vocalizations can potentially convey a variety of information, including age, sex, physical condition, fighting ability, sexual attractiveness, group membership, individual identity, and more (Catchpole and Slater 2008; Jones and Siemers 2011; Searcy and Nowicki 2005). Among the most remarkable function of songs is the ability to encode individual identity. Being able to signal identity, and recognize other individuals is a prerequisite for reciprocity in social animals, and has many potential benefits, for instance it can lead to reduced aggression, improved mating success, increased altruism from kin, etc. (rev. Tibbetts and Dale 2007). Vocal discrimination of individuals seems to be widespread among vertebrates and has been reported in frogs (Bee et al. 2001; Davis 1987), fish (Myrberg and Riggio 1985), dolphins (Janik et al. 2006), primates (e.g., Cheney and Seyfarth 1980; Rendall et al. 1996), elephants (McComb et al. 2000), songbirds (rev. Stoddard

1996), and bats (Boughman and Wilkinson 1998). In bats, individual signatures have been found in three main contexts: mother-offspring recognition (e.g., Balcombe 1990; Bohn et al. 2007; Esser and Schmidt 1989), echolocation signals (rev. Jones and Siemers 2011), and courtship (e.g., Eckenweber and Knörnschild 2013).

Several bat species produce advertisement and/or territorial vocalizations with enough interindividual variation to be able to encode identity; interestingly such vocalizations are not always complex. For example, Seba's short-tailed bat (*C. perspeciliata*) produce a relatively simple courtship call, composed of a repetitive train of a single trill syllable, yet statistical analysis suggest that these courtship trills contain individual signatures (Knörnschild et al. 2014). Similarly, the endangered Seychelles sheath-tailed bat (*C. seychellensis*) emits individually distinctive monosyllabic calls used in mate guarding (Gerlach 2009). Bats whose song is more structurally complex have also been reported to have the potential to encode for individual identity, for instance the territorial song of the greater sac winged bat (*S. bilineata*) encodes individual signatures (Davidson and Wilkinson 2002a; Eckenweber and Knörnschild 2013), Considerable variation in call structure has also been reported for the advertisement calls of the *P. nathusii* (Russ and Racey 2007). While individual variation in vocalizations has been reported for these species, few studies have examined whether bats detect individual signatures and discriminate among individuals (but see Fernandez et al. 2014).

In addition to varying at the individual level, songs can also vary among geographic locations. Regional variation in songs has been of interest to biologists for several decades, discernable differences in songs of birds from different areas have been reported for over a century, but it was not until the advent of the sound spectrograph in the 1950s that these differences could be rigorously quantified. Population specific songs, "vocal dialects" has been found to varying degrees in a wide range of species. Some of the most prominent taxa include songbirds (Marler and Tamura 1962, 1964), parrots (e.g., Marler and Tamura 1962), hummingbirds (e.g., Saunders 1983; Wright 1996), and cetaceans (Gaunt et al. 1994) all of these tend to have complex vocalizations, and have been shown to be capable of vocal production learning. Vocal production learning is the ability to create and/or modify vocalizations in response to social interaction (e.g., Ford 1991; Whitehead 1998), and it can lead to the evolution of stark vocal dialects. Aside from vocal learning, regional differences in vocalizations may arise due genetic differentiation among populations, or as the result of other unrelated selection pressures, for instance vocal signals are often under pressure for optimal acoustic transmission (Morton 1975; Slabbekoorn and Smith 2002) and so populations that inhabit different habitats may be under divergent acoustic selection which results in differences in vocalizations. While geographic variation in echolocation signals has received considerable attention (e.g., Aspetsberger et al. 2003; Guillén et al. 2000; Law et al. 2002; Murray et al. 2001; O'Farrell et al. 2000), geographical variation in bat courtship vocalizations has been largely unexplored. To date, geographical variation in territorial songs has only been reported for the greater sac winged bat (Davidson and Wilkinson 2002). Since individual signatures and vocal dialects are such well-studied phenomena in other taxa, we compare these phenomena in *T. brasiliensis* and *N. laticaudatus*.

6.4 *T. brasiliensis* and *N. Laticaudatus*

6.4.1 Behavior

T. brasiliensis

Brazilian free-tailed bats (*T. brasiliensis*) are small (approximately 10 g) insectivorous molossids that are one of the most abundant and widely distributed bats in the Western Hemisphere. They range from coast to coast of the central United States south to much of South America (Wilkins 1989). In the southwestern and central United States, *T. brasiliensis* parous females migrate from central Mexico to the southern and central United States in the summers forming immense maternity colonies (Glass 1982; Villa and Cockrum 1962) with up to 20 million individuals (Davis et al. 1962).

Mating behavior in *T. brasiliensis* has been difficult to observe due to the migratory behavior and dense aggregations within roosts. All mating was believed to occur in winter months in roosts in Mexico (Davis et al. 1962) until a study described mating activity in transient roosts in Austin, Texas where a promiscuous mating system was observed with no evidence of male territoriality (Keeley and Keeley 2004). This is in contrast to our observations of singing associated with territoriality and courtship during mating at two captive colonies (Austin and College Station) and in the wild at an immense male-dominated year-round roost at Texas A&M in College Station.

Our most extensive observations from individuals are from a captive colony in Austin, Texas (Bohn et al. 2008). This colony had approximately a 5:1 ratio of females to males and approximately 50 bats (although turnover constantly occurred). Songs were only produced during the mating season (February–April). At this time males also established territories that they shared with females but vigorously and aggressively defended against encroaching males. During the remainder of the year there were no territories, aggression was rare, there were no copulations, and the sexes freely intermixed into multi-male-multi-female groups. Thus, songs in Austin were associated almost exclusively with mate attraction and territorial defense during the mating season (Bohn et al. 2008).

Whereas in Austin, the majority of bats in the area are migratory females (the Congress Street Bridge is a maternity colony) the Texas A&M colony, with up to 300,000 individuals, is inhabited almost exclusively by adult males, the majority of which remain throughout the year. We captured bats year round for our captive colony at Texas A&M over a 5-year period. The only times females are present at Kyle field is en masse in early spring (late February–early April) and again in the fall along with juveniles (September–October) presumably migrating to and from winter sites in Mexico to summer maternity colonies. At the Texas A&M roost, bats resided in linear cracks of cement in the football stadium. Males sang at low levels year around at specific locations lined along the cracks at least 15 cm from each other (pers. observ.) During the spring singing intensifies—we recorded 1000's of songs per day (Bohn et al. 2013). In our captive colony of males from the football stadium, males defended roost tubes and sang in both mixed-sex and male-only colonies.

We used playback experiments to examine what triggered singing (Bohn et al. 2013) and found that although conspecific song did not induce singing, echolocation calls of a passing bat did. In fact, bats responded to nearly every echolocation playback extremely rapidly (within 0.5 s). These results are consistent with bats advertising their locations to potential mates or competitors as they fly past. Together these observations indicate that the mating system in *T. brasiliensis* can vary from promiscuity to resource defense polygyny, where males defend roosting territories from other males while advertising and permitting females to reside. Interestingly this is consistent with their relative testes size, which is intermediate between single-male/multi-female groups and multi-male/multi-female groups (Wilkinson and McCracken 2003). Although it seems unlikely that roosting sites were limited at the Texas A&M football stadium, given observations of forced copulations in *T. brasiliensis*, sometimes resulting in injury (Keeley and Keeley 2004), male guarded locations may provide reproductive females refuge from high numbers of potentially aggressive sexually active males.

N. laticaudatus

N. laticaudatus is a similar sized nonmigratory tropical Molossid (12 g) that ranges from northern Mexico southern Brazil (Avila-Flores et al. 2002). They roost in cracks of rocks, tree hollows and in urban ambient inside abandoned buildings. *N. laticaudatus* tends to form big colonies of 1000 s of individuals with small labile roosting groups of 15–30 (Avila-Flores et al. 2002; Ortega et al. 2010). Mating season occurs in February and March when several individuals have been observed to mate indistinctively with more than one partner. Thus, like *T. brasiliensis*, *N. laticaudatus* is considered a promiscuous species (Ortega et al. 2010; Ortega and Martínez-Rodríguez 2011), however, observing mating is also exceedingly difficult. Ortega et al. (2010) observed seasonal differences in behavior, particularly during the mating season, when males more aggressively defended roost sites and females reduced roost-to-roost movement. Males were also observed aggressively defending roost sites against males while permitting females to reside (Ortega and Martínez-Rodríguez 2011). These observations indicate that the mating system may be a combination of promiscuous and resource defense polygyny as in *T. brasiliensis*. Additionally, we observed females to move from inner chambers of the ruins at Uxmal that had very large groups of males to smaller roosting crevices in the outer walls where we recorded male vocalizations in evenly spaced locations as in *Tadarida*. Thus, females may prefer to roost in these less dense regions that are defended by individual males.

To elucidate whether the vocalizations we recorded were associated with mating (i.e., functionally they were songs), we performed echolocation pass and song playbacks at roost sites that were analogous to those conducted on *T. brasiliensis*. In addition we performed playbacks during the mating season (February) and non-mating season (October). If the vocalizations were songs then echolocation playbacks should induce singing, like *T. brasiliensis* and we should record greater singing rates during the mating season. We performed 10 playbacks of each type in the mating season, and 14 song and 15 echo playbacks in the non-mating season and we measured the number of songs produced per second recorded before (pre) and during playbacks (post; Fig. 6.3). Bats responded to playbacks with songs, but only during the mating season (repeated measures ANOVA; pre/post * season interaction; $F_{1,45} = 16.0$, $p = 0.0002$; pre/post, $F_{1,45} = 36.3$, $p < 0.0001$, Fig. 6.3). Overall calling was greater during the mating season (season, $F_{1,45} = 16.6$, $p = 0.0002$). However, there was no difference in responses to songs or echolocation calls, that is, stimulus type had no effect on responses ($F_{1,45} = 0.05$, $p = 0.8$). These results support a courtship function to *N. laticaudatus* songs. However, *N. laticaudatus* respond differently to conspecific song than *T. brasiliensis* indicating that the specific way in which songs are used in the two species differ, especially with respect to interactions among singing males.

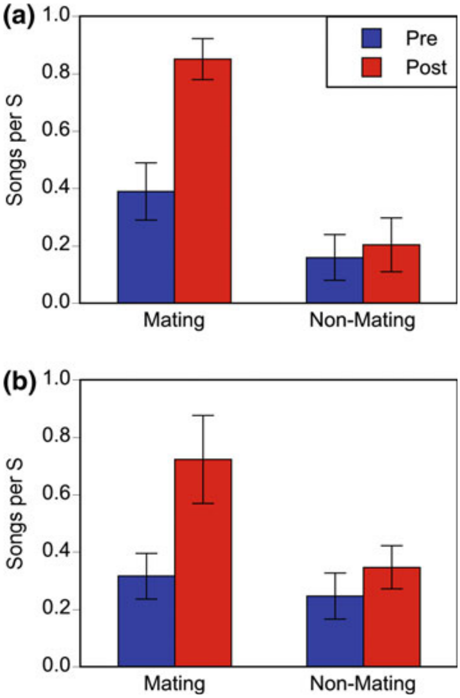


Fig. 6.3 Number of *N. laticaudatus* songs recorded prior to (pre) and during (post) echolocation (*top*) and song (*bottom*) playbacks during the mating season (February, $N = 10$ playbacks of each type) and non-mating season (October $N = 15$ echo and 14 song playbacks). **a** Echo playback. **b** Song playback

6.4.2 Songs

T. brasiliensis songs are hierarchically structured with four types of syllables that are combined to form three types of phrases that are in turn combined to form songs (Fig. 6.2). *Chirp* phrases are composed of varying numbers of *Chirp A* syllables that are punctuated by *Chirp B* syllables. A syllables are downward frequency modulated (FM) sweeps, whereas B syllables are longer and with greater variation in frequency modulation (Bohn et al. 2008, 2009). *Trill* phrases and *buzz* phrases are composed of rapid downward FM syllables of only one general type for each phrase (e.g., *trill syllables* and *buzz* syllables). Two components of songs are no different than components of their echolocation system. Chirp A syllables are no different than echolocation pulses produced in cluttered environments (Bohn et al. 2008) and buzz phrases are no different than feeding buzzes (Schwartz et al. 2007).

One of the most interesting features of this system is song flexibility. Even though song construction follows basic rules, *T. brasiliensis* dynamically vary syllable number, phrase order, and phrase repetitions from one rendition to the next. We use the term *song type* to this variation where each song type is a unique combination of phrases with trill or buzz repetitions excluded (Fig. 6.2). Males can have large repertoire sizes (up to 20 different song types, up to 57 songs recorded per male) even though many song types are shared by the majority of males (Bohn et al. 2008, 2009).

Nyctinomops laticaudatus songs are also composed of chirp, trill, and buzz phrases. However, chirp phrases are alternating B-A syllables and A syllables are not merely down FM sweeps (Fig. 6.2 top two songs). Both chirp A and B syllables are much longer in *N. laticaudatus* than *T. brasiliensis* (Fig. 6.2 and Box 1). In contrast to *T. brasiliensis*, *N. laticaudatus* do not have large song type repertoires. We examined 414 songs from Uxmal and counted only 9 song types, which is much lower than the 36 song types out of 319 songs we found in *T. brasiliensis* (Bohn et al. 2009). The largest repertoire we recorded in an individual *Nyctinomops* was only seven song types (up to 80 songs recorded per male). Seventy percent of songs were chirp only, while another 19 % were buzz-chirp songs. Finally only ~10 % of *Nyctinomops* songs contained trills compared to approximately 50 % of *Tadarida* songs (Bohn et al. 2009).

6.4.3 Individual and Regional Variation

We examined individual and regional variation of acoustic features of five Chirp A and five Chirp B syllables at two locations for each species; *T. brasiliensis* in Austin and College Station, Texas (~140 km, $N = 15$ and 16 males, respectively) and *N. laticaudatus* in Uxmal and Antigua, Mexico (~700 km, $N = 10$ and 11 males, respectively). We used a nested random effects model with individual nested within location for each species and Bonferroni corrections for each syllable type (type B, four variables, alpha = 0.012, type A three variables, alpha = 0.017). We found very different patterns between the two species. Individual *T. brasiliensis* showed extreme repeatability in spectral and spectro-temporal feature of Chirp B syllables with differences across males accounting for as much as 90 % of Chirp B variation, while variation across renditions for an individual male as were as low as 10 % (Table 6.1, all $F_{29,124} > 6.1$, $p < 0.0001$). The same was true for Chirp A syllables although repeatability was not as pronounced. There were no differences between regions for Chirp B syllables (all $F_{1,29} < 3.2$, $p > 0.10$) but a difference was found between the sites in the duration of Chirp A syllables ($F_{1,29} = 7.2$, $p = 0.012$). In *N. laticaudautus*, although features varied significantly across individuals (all $F_{19,84} > 3.3$, $p < 0.0001$) syllables were much less repeatable, in fact there was often more residual variation within individuals than among individuals (Table 6.1). However, *N. laticaudatus* showed much greater regional variation in syllable acoustics than *T. brasiliensis* with as much as 79 % of variation occurring across regions (Table 6.1). Thus, while individual *T. brasiliensis* use highly stereotyped B syllables, that may be considered individual signatures, they show nearly now regional differences. *N. laticaudautus* on the other hand produce regionally distinctive syllables that are less stereotyped within individuals (Table 6.2).

Table 6.2 Residual maximum likelihood variance components estimates from nested random effects ANOVAs chirp syllable acoustics[a]

	T. b		*N. l*	
	Regional	Individual	Regional	Individual
Chirp A				
dur	16*	34	**79*****	5
fmin	15	55	0	57
fmax	0	**70**	0	59
Chirp B				
dur	0	51	23*	27
fmin	5	**89**	24*	35
fmax	0	**89**	17	29
lmin	11	**73**	25**	21
lmax[a]	0	**91**	–	–

These are the percent variation in each measurement attributable to individuals and regions. Individual was significant in all cases ($p < 0.0001$). Components greater than 70 % are in bold. Note that variation within individuals (residual) = 100 − regional − individual

* $p < 0.017$ (significant under Bonferroni post hoc correction)

** $p < 0.001$

*** $p < 0.0001$

[a] Variable was bimodal for indicated species

6.5 Conclusions and Future Directions

Although both Molossid species we investigated have similar song characteristics, we found high noteworthy differences between the two species, which likely reflect different evolutionary pressures between the species (Table 6.3). *N. laticaudatus* have simpler songs with much lower syntactical diversity and complexity than *T. brasiliensis*. This may be due to female preference, as it has been hypothesized that female preference drives repertoire size in songbirds (Catchpole 1987; Collins 2004). However, an alternative hypothesis is that the complexity of interactions, and hence types of "messages" drive larger repertoires (Byers and Kroodsma 2009). Our finding that different song types are used in different social contexts in *T. brasiliensis* supports this alternative (Bohn et al. 2013). Bats may provide a new comparative model for testing these alternative hypotheses for repertoire size. Our second major finding was that *N. laticaudatus* had regional dialects but little stereotypy, the opposite of *T. brasiliensis*. These results indicate that individual identity is not crucial in *N. laticaudatus* song. Moreover, the high variation in

Table 6.3 Summary table of ecology and song features of *N. laticaudatus* and *T. brasiliensis*

	T. brasiliensis	*N. laticaudatus*
Ecology and behavior		
Migratory	Yes	No
Size	10 g	12 g
Colony size	100,000's	1000's
Mating	Promiscuous/resource polygyny	Promiscuous/resource polygyny
Increased singing during mating season	Yes	Yes
Respond to echolocation playbacks	Yes	Yes
Respond to song playbacks	No	Yes
Song syntax		
Number of chirp A's per B	0–15	0–1
Phrases types	3	3
Syllable types	3	3*
Use of trills	High	Low
Song type diversity	High	Low
Syllable acoustics		
Regional B variation	No	Yes
Individual B stereotypy	High	Low
Regional A variation	No	Yes
Individual A stereotypy	Medium	Low

*Chirp B syllables may be multiple discrete types in *N. laticaudatus*

N. laticaudatus chirp syllables and stark vocal dialects indicate they may be good candidates for vocal learning. If this is the case then future comparisons between these two species will be particularly fruitful.

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Chapter 7
Acoustic Communication and Group Cohesion in Spix's Disc-Winged Bats

Gloriana Chaverri and Erin H. Gillam

Abstract Acoustic communication is an especially important means by which social and highly mobile organisms, such as bats, locate group members. Contact calls are known to be used by many species of bats, including those that use permanent roosting structures; these roosts may facilitate group cohesion because individuals can rely on spatial memory and fidelity to a roosting location to relocate group members. However, the neotropical insectivorous bat *Thyroptera tricolor* is known to form extremely cohesive social aggregations despite moving daily between roost-sites. This species uses developing tubular leaves of plants such as *Heliconia* species that unfurl in a few hours, rendering them unsuitable in less than 24 h. Our research shows that *T. tricolor* uses a combination of two social signals, "inquiry" and "response" calls, to locate each other during flight and while roosting. Individuals may recognize, and be able to preferentially associate with, group members due to strong individual signatures in these two types of calls; group cohesion may be further facilitated by recognition based on spatial location, as this species uses small roosting home ranges and exhibits extreme philopatry to the natal territory. Coupling spatial memory with acoustic communication may be an especially effective mechanism of recognition in this system, as tubular roosts cause significant distortion of acoustic signals used during contact calling. The tubular leaves, however, also provide a significant increase in signal amplitude that may allow bats to locate each other over longer distances. Our work with *T. tricolor* not only highlights the important role that social calls play in maintaining cohesive groups in highly mobile species, but the role that roosting structures may play in facilitating sociality in bats.

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7.1 Introduction

Bats are highly social animals, with many species living in groups of varying size and social structure (McCracken and Wilkinson 2000). In line with this high level of sociality, bats have been found to use a variety of communication signals for exchanging a diversity of information between conspecifics (Gillam and Fenton 2016). Although most signaling modalities are used by bats, the dominant communication system often appears to be acoustic in nature. This is not surprising given the limited value of visual signals for animals that are nocturnal and live in tight, dark places with minimal light exposure. Further, flight means that bats can move quickly through their environment, so the rapid transmission speed and long potential range of acoustic signals makes sound an optimal modality for communication in this taxon.

When surveying the bat acoustic literature, there has clearly been a strong bias toward studying echolocation (Schnitzler et al. 2003; Jones and Teeling 2006; Fenton 2013). In the past two decades, research on the social calls of bats has flourished, with studies asking a variety of proximate and ultimate questions ranging from the behavioral function of social calls (i.e., Barlow and Jones 1997; Behr et al. 2006), to the neurobiology behind signal processing (i.e., Moss and Sinha 2003; Simmons 2012). The results have revealed a rich field of scientific inquiry, of which we have only begun to scratch the surface.

Social calls in bats have been shown to serve a variety of behavioral functions. In several species, males produce complex, stereotyped songs for attracting females (i.e., Behr and von Helversen 2004; Bohn et al. 2009). In at least ones species, the complexity of an individual male's song is directly linked to mating success (Davidson and Wilkinson, 2004). Territorial signals to repel conspecifics have been reported in several species; in some cases, these calls are involved in male–male competition (Behr and von Helversen 2004; Eckenweber and Knörnschild 2013), while in others, calls are produced in defense of foraging sites (Barlow and Jones 1997; Georgiakakis and Russo 2012), particularly during periods of low food abundance. Agonistic calls associated with human handling or aggressive conspecific encounters are also commonly reported (Bastian and Schmidt 2008; Bohn et al. 2008). During encounters with predators, several bat species produce distress calls that attract nearby conspecifics (Fenton et al. 1976; Hill and Greenaway 2005), presumably for predator mobbing (Knörnschild and Tschapka 2012).

A particularly fascinating area of research addresses how bats use social calls to locate other bats in the nearby area. Given the tendency for bats to rapidly fly through their environment, individuals invariably become separated from conspecifics. It is well known that in maternity colonies, females often rely on isolation calls produced by pups to locate their own offspring (Balcombe 1990). In all cases studied to date, each pup has a unique isolation call structure (Gelfand and McCracken 1986; Scherrer and Wilkinson 1993), making this an ideal signal for females to discriminate their own pup from others. In many species, social calls are also used for maintaining group cohesion. Production of such signals, known as contact calls, is common in other taxa, and is often a critical mechanism supporting maintenance of social groups. Antiphonal exchange of contact calls between conspecifics has been reported in multiple bat species (Boughman and Wilkinson 1998; Arnold and Wilkinson 2011; Carter et al. 2012). Yet, all of these species use permanent or semi-permanent roosting structures, which should allow bats to use spatial memory of the roost-site to facilitate reunion with group members. Building upon this observation, we were interested in understanding the role of contact calls in species that use highly ephemeral roosts—such a roosting ecology means that individuals cannot simply return to the last roosting site to locate group members, as that roost is likely to be defunct and no longer in use by other bats.

7.2 The Conundrum

Spix's disc-winged bat (*Thyroptera tricolor*) is a small (c.a., 4 g) insectivorous bat whose main diagnostic characteristic is the possession of sucker-like structures on its hands and feet that make it highly specialized for holding on to the smooth surfaces of structures that are used as roosting habitat (Wimsatt and Villa-R 1970; Wilson and Findley 1977); as a result, they likely are incapable of using other structures that require gripping (Riskin and Fenton 2001). In fact, *T. tricolor* is known to roost almost exclusively inside the developing furled leaves of plants of the order Zingiberales, particularly those in the genus *Heliconia*, but also in other species such as *Musa* spp. and *Calathea* spp. (Fig. 7.1; Findley and Wilson 1974; Vonhof and Fenton 2004; Chaverri and Kunz 2011b). These developing tubular leaves remain as suitable roosting habitat for very short periods of time. For example, a study by Vonhof et al. (2004) showed that tubular leaves remain within

Fig. 7.1 *Thyroptera tricolor* group roosting within a tubular furled leaf of *Heliconia imbricata*. Photo by Sébastien Puechmaille

the preferred size range between 8 and 16 h. This means that bats must locate a new roost every day. Despite this constant need to search for new roosts, bats use a relatively small roosting home range of 0.14–0.19 ha (Vonhof et al. 2004; Chaverri and Kunz 2011b), as the plants that provide roosting habitat tend to have a patchy distribution. Therefore, some of the obvious costs that a constant search for suitable roosting sites imposes on bats, such as high energetic expenditure and greater exposure to predators during flight (Fenton et al. 1994; Schmidt-Nielsen 1997; Alexander 2002; Thomas and Jacobs 2013), are likely reduced by the distribution and local abundance of roosting habitat. In addition to using a small roosting area, studies suggest that groups are territorial (Findley and Wilson 1974; Chaverri and Kunz 2011b), which could further increase the local availability of roosting habitat.

Despite changing roosts on a daily basis, *T. tricolor* forms and maintains small but very stable social groups (Findley and Wilson 1974; Vonhof et al. 2004; Chaverri 2010). The typical size of social groups, defined here as all individuals that share the same roost at the same time (Fig. 7.1), is 5–6 individuals; few groups are composed of 1 or 2 bats, and maximum group size observed has been 11 bats (Findley and Wilson 1974; Vonhof et al. 2004; Gillam and Chaverri, unpublished data). These social groups are composed of males and females, in varying proportions (Findley and Wilson 1974; Vonhof et al. 2004; Chaverri 2010). The average time that the majority of dyads remain together is 100 days (Vonhof et al. 2004), although group composition can remain unchanged, with no immigration or emigration, for up to 22 months (Chaverri 2010). Relatedness among group members is extremely high (Buchalski et al. 2014), and groups are composed mainly by philopatric individuals; results of long-term studies of group dynamics indicate that bats remain within their natal territory and group for several years (Chaverri and Kunz 2011a), even after they have acquired reproductive maturity (Chaverri and Vonhof 2011). All these findings on group dynamics in *T. tricolor* suggest high benefits of philopatry and/or high costs of dispersal, and pose an interesting question on how such groups are capable of remaining together despite constant roost switching.

As a taxonomic group, bats use many different roosting resources that vary in permanence. Many species of bats use caves, which can remain as suitable roosting habitats for very long periods of time, whereas other species use ephemeral roosting resources such as modified leaves or tent-roosts that can last short periods of time of only a few weeks (Kunz 1982; Lewis 1995; Altringham 2011). Studies suggest that the permanence of these resources may affect roost fidelity (Lewis 1995), which in turn affects group cohesion (Lewis 1996), such that more permanent roosts are associated with more cohesive groups. Several species, however, do not fit the above pattern (e.g., Chaverri and Kunz 2010), including *T. tricolor*. This latter species uses the most ephemeral roosting structures known, yet exhibits one of the most stable social aggregations. Thus, *T. tricolor* provides one of the best model organisms to understand the mechanisms responsible for maintaining stable social aggregations despite high mobility and a nocturnal life style.

7.3 Use of Contact Calls

As we were conducting studies on patterns of social cohesion and natal philopatry in *T. tricolor* (Chaverri 2010; Chaverri and Kunz 2011a), we noticed a puzzling behavior. During our sampling, we would often capture several groups from an area, process them, and then release all individuals belonging to the same group within their roosting territory, while keeping other bats in cloth bags to release in their respective territory. As we released a group, we noticed that instead of flying away, bats would approach us and attempt to land on the cloth bags holding other individuals. This behavior led us to suspect that restrained bats were using ultrasonic acoustic signals to advertise their location, thereby attracting flying bats. Based on these observations, we started a series of experiments in which a single individual was placed inside a tubular leaf, while others were allowed to fly near the roosting bat.

The results of our field experiments to determine if bats were using acoustic signals to locate group members or roost-sites showed that, as soon as bats started to fly, they emitted a simple frequency-modulated signal in addition to their echolocation calls (Fig. 7.2; Chaverri et al. 2010). Because of the function of this call, which presumably is to inquire about the location of roosts or group members, we termed it "inquiry call." We were able to record these inquiry signals in 66 % of acoustic trials; in the remaining 34 % of trials, bats flew away from our study site

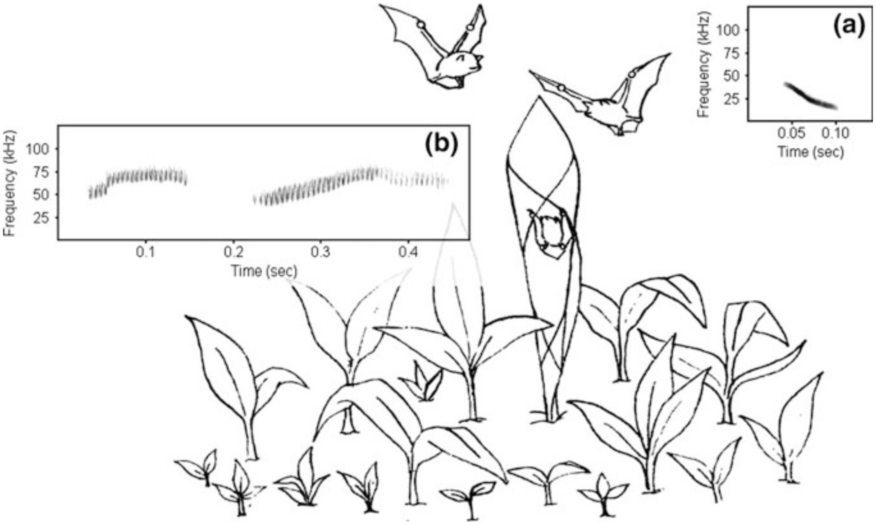


Fig. 7.2 Illustration that depicts the contact calling system in *Thyroptera tricolor*. "Inquiry" calls (sonogram shown in inset **a**) are emitted constantly by flying bats that are seeking suitable roost-sites or group mates. "Response" calls (sonogram shown in inset **b**) are produced in reply to an inquiry call by individuals that have already located a roost, and can be emitted as single calls or in a bout. Illustration by Alexandra Cardenal Cruz (2013)

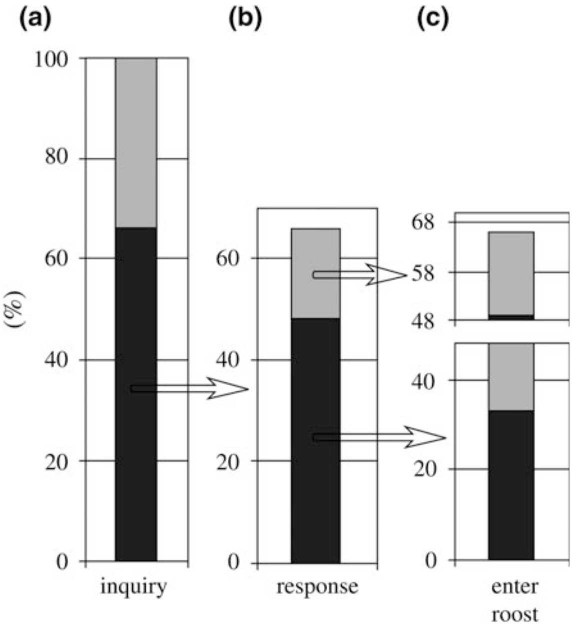


Fig. 7.3 Percentage of times in which a specific behavior was recorded (*black*) or not recorded (*gray*). **a** Occurrence of inquiry calls; **b** occurrence of response calls when an inquiry call was recorded (no response calls were recorded in the absence of inquiry calls); **c** bats entering the roost in the absence (*upper*) or presence (*lower*) of response calls

and were not seen further (Fig. 7.3; Chaverri et al. 2010). When we were unable to record any inquiry calls from flying bats, no other sounds were recorded from bats within the roost. However, in 72 % of cases when bats emitted an inquiry call, bats within a roost quickly "responded" with a complex signal that was emitted in bouts (average of 6.22 calls per bout; Fig. 7.2). Due to the function of this latter signal, we termed it "response call." When the bat within the roost responded, the majority (70 %) of bats flying were able to locate and enter the tubular leaf-roost (Fig. 7.3; Chaverri et al. 2010). These results show that this combination of call-and-response signals allows roosting bats to advertise their location to flying conspecifics, and that their response calls may in turn be critical for rapid location of a refuge by flying individuals.

Based on results of our field experiments (Chaverri et al. 2010), we can conclude that the call-and-response behavior in *T. tricolor* favors rapid location of roost-sites. As tubular leaves quickly become unsuitable for roosting, *T. tricolor* is constantly forced to locate new furled leaves during flight. Compared to other means of locomotion, flight imposes high energetic costs to vertebrates (Thomas and Suthers 1972; Arita and Fenton 1997; Schmidt-Nielsen 1997; Alexander 2002); thus, having more individuals to scan for roosting sites can significantly decrease the costs associated with flight. As the number of individuals that are attempting to locate a similar resource increases, so does the probability of finding such resources because a greater proportion of the territory can be covered (Ward 2012); this ultimately decreases the average individual energetic investment in that activity, because scanning the entire territory by all group members is not necessary once an individual has located a suitable resource. Because roosts also provide bats with a means to avoid predators (Thomas and Jacobs 2013), finding hiding sites promptly also represents an important benefit of the contact calling system employed by *T. tricolor*.

Although the benefits provided by the call-and-response system seem obvious for flying *T. tricolor*, it is not clear how responding bats within roosts may benefit from announcing their location. Some of the benefits of forming groups while roosting may include decreased energetic expenditure in thermoregulation (Scantlebury et al. 2006; Willis and Brigham 2007), a reduced individual investment in predator vigilance (Pulliam 1973; Lima 1995) and dilution of predation risk (Wrona and Dixon 1991), in addition to other benefits such as allogrooming and allofeeding (Mooring et al. 2004; Kalishov and Zahavi 2005). Social thermoregulation often is not considered a major advantage to forming groups in warm tropical regions where ambient temperatures are generally high, and individuals must actually develop physiological adaptations to help them cope with high temperatures (Weathers 1997). Thus, because *T. tricolor* inhabits the warm lowland forests of the Neotropics (Wilson and Findley 1977), many of the benefits acquired by recruiting mates to roost-sites by *T. tricolor* are likely not related to thermoregulation. In contrast, rapid response to predator attacks with a reduced individual investment in vigilance could be an important benefit of recruiting roost-mates in *T. tricolor*. The topic of decreased vigilance in larger groups has seen mixed results (Beauchamp 2008), however, studies suggest that individuals respond faster to predator attacks if they rest in groups, and not solitarily (Semeniuk and Dill 2005).

In addition to predator avoidance, *T. tricolor* could benefit from recruiting roost-mates if these provide care through allofeeding or allogrooming. Allofeeding has been observed in several bat species (Wilkinson 1984, 1992; Geipel et al. 2013), yet whether this kind of social interaction occurs in *T. tricolor* remains to be tested. Allogrooming is common in some species of bats (Kerth 2008), and may be particularly important in reducing parasite load when colonies suffer high rates of ectoparasite infections (Bordes et al. 2007; Hillegass et al. 2008). *T. tricolor* is not commonly afflicted by high ectoparasite loads, as their roosting sites are exposed and ephemeral (ter Hofstede and Fenton 2005; Patterson et al. 2007), which suggests that allogrooming is not common nor highly beneficial in this species.

The probability of occurrence of costly behaviors, such as allogrooming and allofeeding, increases when interacting individuals are genetically related (Hamilton 1964), or if individuals have created strong social bonds through repeated interactions (Axelrod and Hamilton 1981; Grabowska-Zhang et al. 2012; Carter and Wilkinson 2013). Repeated interactions may occur when individuals consistently use the same roosting and foraging sites (Garroway et al. 2013), either through philopatry or site fidelity, or if individuals are able to discriminate and preferentially associate with the same set of conspecifics (Keen et al. 2013; Sharpe et al. 2013). Thus, while the call-and-response system employed by *T. tricolor* may allow individuals to locate other roosting bats, in order to maintain contact with the same members, individuals must employ some form of recognition mechanism.

7.4 Mechanisms for Recognition of Group Members

The mechanisms that animals use to recognize group and nongroup members include spatial location, familiarity, phenotype matching, and recognition tags (Mateo 2004; Bradbury and Vehrencamp 2011). Spatial location is the simplest process of recognition, whereupon individuals associate a specific location with one or several target individuals; helping behaviors are focused on individuals that inhabit that particular place (Bradbury and Vehrencamp 2011). Familiarity, or associative learning, is a mechanism that requires individuals to learn specific characteristics from common associates, and to discriminate familiar from unfamiliar based on signature signals (Bradbury and Vehrencamp 2011; Roberts et al. 2014). Phenotype matching involves the recognition of related and unrelated individuals based on phenotypic similarity, assuming phenotype similarity correlates with genetic similarity (Lacy and Sherman 1983; Grafen 1990; Bradbury and Vehrencamp 2011). Finally, recognition tags involve the genetic predisposition to produce, perceive, and aim cooperative interactions toward individuals with a specific characteristic or tag. This type of recognition process does not involve learning, and individuals do not need to share genes at other loci, just a single gene (or set of tightly linked genes) that codes for the recognition tag (Gardner and West 2010; Bradbury and Vehrencamp 2011). While all these recognition mechanisms have some level of empirical support in other taxa, we will only discuss spatial location and familiarity as potential mechanisms for recognition of group and nongroup members in *T. tricolor*.

7.4.1 Spatial Location Through Natal Philopatry

Results of capture–recapture studies in *T. tricolor*, coupled with analysis of genetic relatedness, demonstrate that this species exhibits all-offspring natal group and site philopatry (Chaverri and Kunz 2011a; Buchalski et al. 2014). Models of emigration and mortality, based on recapture rates of three study areas, show that these populations exhibit low emigration rates of 0.36–0.73 individuals per year (Chaverri and Kunz 2011a); this suggests that one individual emigrates out of its natal territory every 1.5–3 years. Offspring of both sexes remain within their natal roost-site and natal group for several years, even after acquiring sexual maturity (Chaverri and Kunz 2011a; Chaverri and Vonhof 2011), which results in high levels of genetic relatedness among group members (Buchalski et al. 2014). Interestingly, preliminary observations suggest that dispersal events in *T. tricolor* are often characterized by the departure of mother–offspring pairs (Chaverri and Kunz 2011a). This type of dispersal, whereupon individuals disperse as a group, is referred to as budding-dispersal, and apparently favors cooperation since this reduces local competition while increasing the chances of new groups being composed of related individuals (Pollock 1983; Goodnight 1992; Wilson et al. 1992; Kümmerli et al. 2009).

The above results suggest high costs to dispersal or large benefits of philopatry in *T. tricolor*. *T. tricolor* has a wing-shape mainly designed for slow, maneuverable flight, which may impose large costs to long-distance flights (Norberg and Rayner 1987). Also, because *T. tricolor* is highly specialized in using plants with a patchy distribution (Stiles 1975; Riskin and Fenton 2001), and because groups are territorial (Chaverri and Kunz 2011b), locating new empty patches may be extremely difficult, thereby further favoring philopatry (Johnson and Gaines 1990). In addition to these costs, an important benefit to remaining philopatric is that interactions at the roost occur mostly among the same, closely related, individuals, which may increase the chances of cooperative interactions (Hamilton 1964; Axelrod and Hamilton 1981; Grabowska-Zhang et al. 2012; Carter and Wilkinson 2013).

The results of natal philopatry in *T. tricolor* suggest that repeated interactions among the same group members are at least partly explained by the consistent use of the same roosting areas. However, using the same roosting territory does not preclude interactions among individuals of different groups, particularly because some overlap of territories is common (Vonhof et al. 2004). Therefore, the fact that *T. tricolor* has such high levels of group cohesion (Vonhof et al. 2004; Chaverri 2010) suggests that other mechanisms may be responsible for keeping the same group members together over long periods of time, and that these mechanisms entail some form of recognition among group members.

7.4.2 Familiarity and Signature Signals

Organisms use a diversity of signal types for maintaining contact among specific individuals, such as mother–offspring, mating partners, or group members (Bradbury and Vehrencamp 2011; Stevens 2013). Acoustic signals are particularly useful when individuals must locate partners over long distances (Naguib and Wiley 2001; McComb et al. 2003), and they have the potential to encode various kinds of social information, including location of the sender, as well as identity and group membership, which allows individuals from the same group to remain cohesive while recognizing potential competitors or intruders (Kondo and Watanabe 2009). Recognition of group members through contact calls can occur via signal convergence due to genetic similarity (Price 1999), socially mediated changes or learning (Sharp and Hatchwell 2006), or individual recognition based on familiarity (Kondo et al. 2010).

The acoustic signals that *T. tricolor* uses for locating roosts and roost-mates are a good candidate for exploring the role of signature signals in maintaining cohesive groups. We recorded inquiry calls of 104 bats belonging to 30 different social groups, and response calls of 34 bats from 14 groups, and found that calls emitted by *T. tricolor* during flight and while announcing roost location are similar within, but different between, individuals, which potentially allows recognition of individual bats based on the structure of these acoustic signals. For inquiry calls, the most important acoustic parameters that help differentiate individual signals are call duration and frequency at the start of the call, whereas for response calls the most important parameters are peak frequency at the start of the syllable, and the inter-syllable interval (Gillam and Chaverri 2012). Analyses of information capacity, the amount of information that can potentially be encoded in a signal, resulted in values of 1.95 for inquiry calls and 3.65 for response calls. These findings suggest that the number of unique signatures that can be encoded in each call type is approximately 4 for inquiry calls, and 13 for response calls (Chaverri et al. 2013). While these results show that inquiry and response calls emitted by *T. tricolor* have a sufficiently broad parameter space for individual recognition to occur within a group, they do not confirm that this species can discriminate between individuals and groups (Gillam and Chaverri 2012).

We conducted a series of experiments to test if individual recognition in *T. tricolor* occurs based on acoustic signals (Chaverri et al. 2013). Inquiry calls are commonly emitted by bats during flight, and group members are often seen flying together as they are scanning their territories for a new roost-site (Chaverri and Gillam, personal observation). We observed that individuals preferentially approached broadcast signals from group members during flight (Fig. 7.4a). In another set of experiments, we also wanted to test if flying bats would preferentially enter leaves from which a bout of response calls from a group member was being emitted. Our results show that when two exact roost options that differ in the calls that are being broadcast from them are presented to flying bats, individuals prefer to enter the leaf with a call from a group member (Fig. 7.4b). In our final experiment, our aim was to determine if roosting bats would preferentially respond to inquiry calls from group members. We placed a bat inside a tubular leaf, and broadcast inquiry signals from group and nongroup members. To our surprise, bats responded equally to both sets

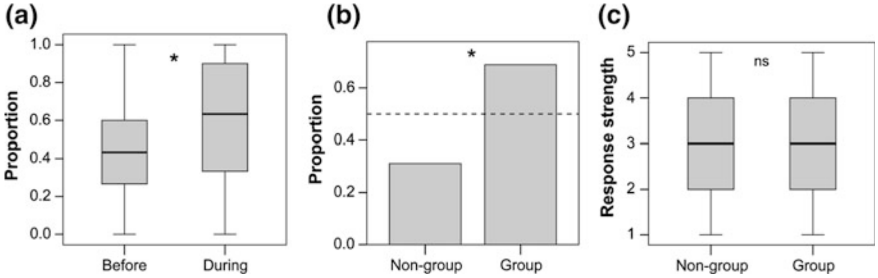


Fig. 7.4 **a** Proportion of time bats spent in the side of the flight cage where an inquiry call of a group member was emitted during the experiment. Bars represent results before and during sound reproduction. *Asterisk* denotes a significant increase in time spent near the speaker where an inquiry call from a group member was being broadcast during sound reproduction. **b** Proportion of times bats entered leaves where a response call from a nongroup and group member was broadcast. *Asterisk* denotes a significant preference to enter leaves from which a call from a group member was being emitted, based on the null expectation that bats would enter either leaf with equal proportions. **c** Average response strength of bats to inquiry calls from nongroup and group members. The difference in mean response strength to nongroup and group members was not significant

of calls (Fig. 7.4c). These results suggest that during flight, *T. tricolor* can recognize inquiry and response signals from flying and roosting group members, respectively, and preferentially approach the source of this familiar signal. In contrast, roosting bats do not seem to recognize, or refuse to respond preferentially to, inquiry calls from group members (Chaverri et al. 2013). Despite this latter finding, our results show that contact signals with strong individual signatures facilitate the relocation of group members in *T. tricolor*.

7.5 Roosting Environment and Social Communication

The results of acoustic signal recognition in *T. tricolor* suggest that bats inside tubular leaves are unable to recognize, or do not exhibit a preference to respond to, inquiry calls from group members; this could potentially be explained by the lack of sufficient information in the inquiry signal to permit efficient assessment of individual identity (Gillam and Chaverri 2012; Chaverri et al. 2013). However, experiments of individual discrimination show that flying bats appear to discriminate inquiry signals from group and nongroup members, preferentially joining the former (Chaverri et al. 2013), which suggest that despite a lower information capacity of inquiry signals, bats are capable of recognizing group from nongroup members based on these calls. The main difference in the experimental setup that could explain a lack of discrimination of inquiry signals is the presence of the tubular leaf; bats can recognize inquiry calls when they detect them during flight, but cannot seem to recognize individual identity when they are inside the tubular leaf.

To test the hypothesis that tubular leaves affect signal fidelity, we conducted a series of acoustic experiments with inquiry and response calls that we had previously recorded from bats in the field (Chaverri and Gillam 2013). In the "incoming inquiry" experiment, we broadcast inquiry calls into a tubular leaf, and measured how parameters of the call changed compared to the signal recorded with no leaf. Then we conducted a second experiment called "outgoing response," where we broadcast response calls from within a tubular leaf, and compared call parameters with the signal recorded with no leaf. Our results show that both inquiry and response calls experience significant distortions in spectral parameters (Fig. 7.5), some of which are important for differentiating individual signals (Gillam and Chaverri 2012). These results explain why roosting bats may have difficulties discriminating between the inquiry calls from group and nongroup members. Notwithstanding, flying bats can discriminate between the response calls emitted by group and nongroup members within the roost, probably because response calls are more complex signals that carry a larger amount of information, and can still be recognized even after being degraded by the tubular leaf (Chaverri and Gillam 2013).

Although the tubular leaves used by *T. tricolor* for roosting significantly affect signal fidelity, as shown above, they also may play an important role in enhancing sound transmission. These tubular structures resemble acoustic horns, which historically have been used by humans for amplifying incoming and outgoing sounds

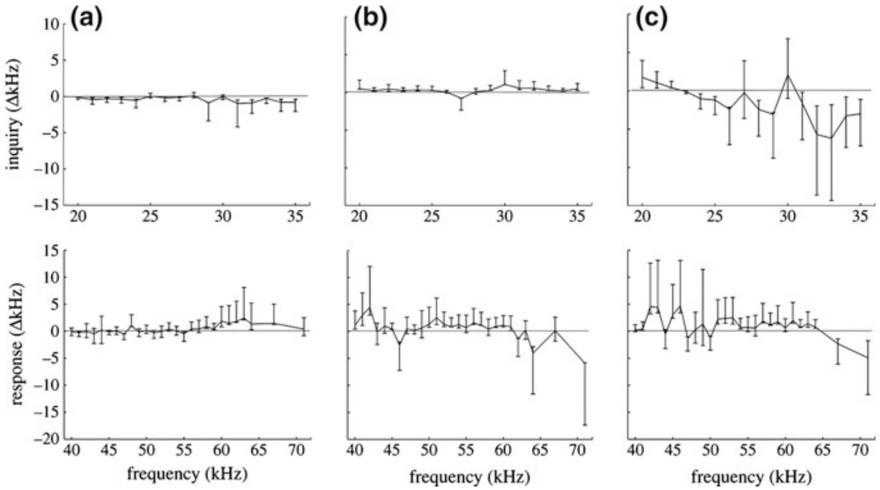
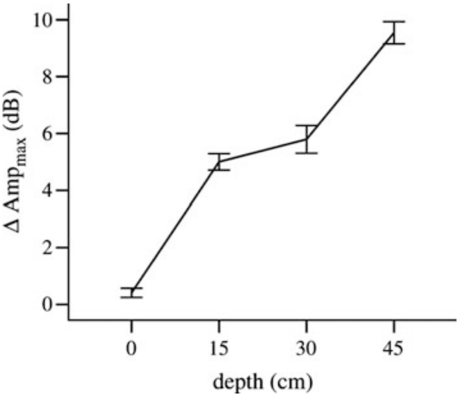


Fig. 7.5 Mean difference in call frequency (in kHz) between experimental (*leaf*) and control (*no leaf*) trials for inquiry and response calls. Horizontal axis represents the original frequency of broadcast calls, based on signals recorded during control trials. *Vertical lines* represent the 95 % bootstrap confidence intervals (CIs) for each frequency. The *horizontal line* represents a mean value of 0. CIs that cross the 0 line for both types of call represent a frequency for which no differences between experimental and control trials were observed. **a** F_{start}, **b** F_{end}, and **c** $F_{\max}$

(Mills 2009). In fact, the "incoming inquiry" experiments explained above demonstrate that calls are significantly amplified as they enter the tubular leaf, particularly as the microphone was placed deeper within the tubular structure (Fig. 7.6; Chaverri and Gillam 2013), a position typically chosen by *T. tricolor* for roosting. An increase in 10 dB for calls within the 20–25 kHz range, such as the inquiry signals used by *T. tricolor* (Chaverri et al. 2010), means that these signals may travel an additional 20–30 m (International Organization for Standarization 1993). This additional distance conferred by tubular leaves certainly represents an important means to facilitating the relocation of group members.

Fig. 7.6 Difference in call amplitude ($\text{Amp}_{\max}$) in decibels for inquiry calls according to the position of the microphone within the leaf. The difference represents the mean amplitude of calls emitted into a leaf minus the mean amplitude of calls without a leaf. *Vertical lines* represent the 95 % CIs



7.6 Conclusions

Our work with *T. tricolor* has highlighted the important role that acoustic communication can play in maintaining group cohesion for a bat species that relies on highly ephemeral roosting resources. Overall, we documented the use of a two-signal contact calling system in which both signals exhibit sufficient information capacity for individuals to produce unique call signatures. Discrimination of group *versus* nongroup members based on such signatures does occur, but only among flying bats (individuals within the roost exhibit no preference for the calls of group *versus* nongroup members that are flying in the area). This discrimination bias may ultimately be driven by the constraints of receiving signals within a tubular leaf, which amplifies calls, but also distorts the incoming signal. While some questions have been answered, many exciting questions in this and related systems are still open for inquiry. Here, we discuss two such areas of research: the costs and benefits of calling behavior and patterns of contact calling in other leaf-roosting bats.

When examining individual calling behavior, it was clear that some individuals frequently produced contact calls, while others did not. Further analysis revealed that these differences in calling behavior were consistent over time (Chaverri and Gillam 2015). Such individual repeatability begs the questions—what are the costs and benefits of calling, and why do we see differences among individuals in calling behavior? The primary cost of calling is likely related to the energetic expense of signal production, which has been shown to be significant in other bat species (i.e., Dechmann et al. 2013). Such high costs may be especially true for the long, complex response call of *T. tricolor* that is often produced in bouts. Benefits of contact calling are related to advantages of group living—in the case of *T. tricolor,* further benefits may be achieved due to indirect fitness gains driven by high relatedness among group members (Vonhof 2001; Buchalski et al. 2014). An analysis of variation in calling rates within groups revealed that a given group includes a mix of individuals with different vocal behaviors (i.e., call at high, medium, or low rates; Chaverri, unpublished data). Such adoption of different social roles by animals within a group may represent an optimal compromise between maximizing the ability to locate group mates and minimizing the costs related to the redundancy of social call production (Chaverri, unpublished data). Future energetic studies of signal production will be particularly valuable for understanding variability in calling behavior within groups.

As a second line of inquiry, little is known about how social calling systems are related to patterns of group cohesion in tent-making bats. This category includes a large number of tropical species that modify plant structures to create high-quality roosting areas (e.g., "tents"). These tents vary in their permanency depending upon the plant species used, from a few weeks to several months. Tent-making bats are a particularly interesting group for asking comparative questions about contact calling, as there is variation across species in tent lifespan and social structure, including group size, composition, and levels of group fidelity (Sagot and Stevens

2012); such factors are likely inextricably linked to the evolution of communication systems. For example, Gillam et al. (2013) described contact calls produced in the early morning at the roost by two different species—(1) *Dermanura watsoni*, in which polygynous harem groups are formed, and (2) *Ectophylla alba*, in which mixed sex groups are formed. While observations were limited, *D. watsoni* group formation seemed to be driven primarily by males calling to females from the roost, while *E. alba* calls were more readily produced on the wing in the vicinity of the tent. Expansion of such comparative work to other species would help shed light on links between roost permanency, social structure, and contact calling in bats, as well as other animals.

As our knowledge of the social lives of bats continues to increase, we will gain more insight into the important role that social calling plays in the lives of bats. By identifying links between ecology and behavior within and between species, we can continue to better understand how communication systems have evolved in bats. Where investigated, bats have been shown to exhibit rich call repertoires, yet many open questions remain about signal function, fitness consequences of signaling behavior, and the importance of multimodal signaling, among others. We hope that this chapter inspires other scientists and students of bioacoustics to pursue research on the social calls produced by this fascinating group of mammals.

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Chapter 8
Sexually Selected Vocalizations of Neotropical Bats

Mirjam Knörnschild, Maria Eckenweber, Ahana A. Fernandez and Martina Nagy

Abstract Acoustic signals are by far the best studied component of bats' social communication. Various different vocalization types cover diverse social interactions, which are either under natural selection pressures, such as mother–pup recognition and group cohesion, or under sexual selection pressures, such as male–male aggression, territoriality, and courtship. Here, we summarize the current knowledge about sexually selected vocalizations in Neotropical bats. Specifically, we highlight research findings on sexually selected vocalizations in two species whose social organization and natural history are well understood, namely Seba's Short-tailed Bat *Carollia perspicillata* (Phyllostomidae) and the Greater Sac-winged Bat *Saccopteryx bilineata* (Emballonuridae). Males of both species exhibit resource-defense polygyny and use distinct vocalizations during aggressive male–male interactions and to announce territory ownership. While territorial vocalizations are structurally more complex in *S. bilineata* than *in C. perspicillata*, the latter species uses a more sophisticated, ritualized suite of behavioral displays to mediate male–male aggression than *S. bilineata*. Moreover, males of both species exhibit acoustic courtship which displays with differing degrees of complexity. In *S. bilineata*, courtship vocalizations are long and elaborate, while courtship vocalizations of *C. perspicillata* are comparatively simpler, with one variable syllable repeated in succession. As a synopsis, we discuss whether differences in social organization and behavioral interactions may have implications for the structural complexity and information content of sexually selected vocalizations.

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8.1 Vocalizations of Neotropical Bats Under Different Selection Pressures

Bats' ability to orient and forage by echolocation is enabled by their fine-tuned neural control over their vocal tract (reviewed in Neuweiler 2003). Since echolocation can be a preadaptation for sophisticated vocal communication, bats are an ideal taxon to investigate the interplay of vocal communication and social organization in highly diverse species. Compared to echolocation calls, bats' social vocalizations are still understudied (reviewed in Fenton 1985, Wilkinson 2003). Most investigations focus on selected vocalization types, making studies of species-specific vocal repertoires particularly rare. The few thorough investigations available for Neotropical bats describe the vocal repertoires of only few species, namely Mexican Free-Tailed Bats *Tadarida brasiliensis* (Bohn et al. 2008), Lesser Bulldog Bats, *Noctilio albiventris* (Brown et al. 1983), Pallas's Long-Tongued Bats, *Glossophaga soricina*, and Commissaris's Long-Tongued Bats, *Glossophaga commissarisi* (Knörnschild et al. 2010a), Seba's Short-Tailed Bats, *Carollia perspicillata* (Porter 1979a, b; Straub and Esser 2000; Knörnschild 2014), and Greater Sac-Winged Bats, *Saccopteryx bilineata* (Bradbury and Emmons 1974, Davidson and Wilkinson 2004, Behr and von Helversen 2004).

In contrast to vocal repertoire descriptions, studies focusing on one or a few selected vocalization types are more common; those studies can deepen our understanding of how specific vocalizations are acquired and what selective pressures act on them. Generally speaking, bat vocalizations can either be under natural or sexual selection pressures. Natural selection pressures act on vocalizations produced in the context of mother–pup recognition, e.g., in Greater Spear-Nosed Bats, *Phyllostomus hastatus* (Bohn et al. 2007), Pale Spear-Nosed Bats, *P. discolor* (Esser and Schmidt 1989), *T. brasiliensis* (Balcombe 1990), *C. perspicillata* (Knörnschild et al. 2013), and *S. bilineata* (Knörnschild and von Helversen 2008), or in the context of group cohesion/coordination, e.g., in White-Winged Vampire Bats, *Diaemus youngii* (Carter et al. 2009), Spix's Disc-Winged Bats, *Thyroptera tricolor* (Chaverri et al. 2013), and *P. hastatus* (Wilkinson and Boughman 1998). Sexual selection pressures, on the other hand, act on vocalizations produced in the context of territoriality, male–male aggression, and courtship. Only three Neotropical bat species have been studied thoroughly with regard to their sexually selected vocalizations: Mexican Free-Tailed Bats, *T. brasiliensis* (Bohn et al. 2008, 2009, 2013; see also chap. 6 in this book), Seba's Short-Tailed Bats, *C. perspicillata* (Porter 1979b; Knörnschild et al. 2014, Fernandez et al. 2014), and Greater Sac-Winged Bats, *S. bilineata* (Bradbury and Emmons 1974, Tannenbaum 1975, Davidson and Wilkinson 2004, Behr and von Helversen 2004). The latter two species (Fig. 8.1) shall be used as a case study in this chapter to discuss whether differences in natural history, social organization, and behavioral interactions lead to differences in the structural complexity and information content of sexually selected vocalizations.

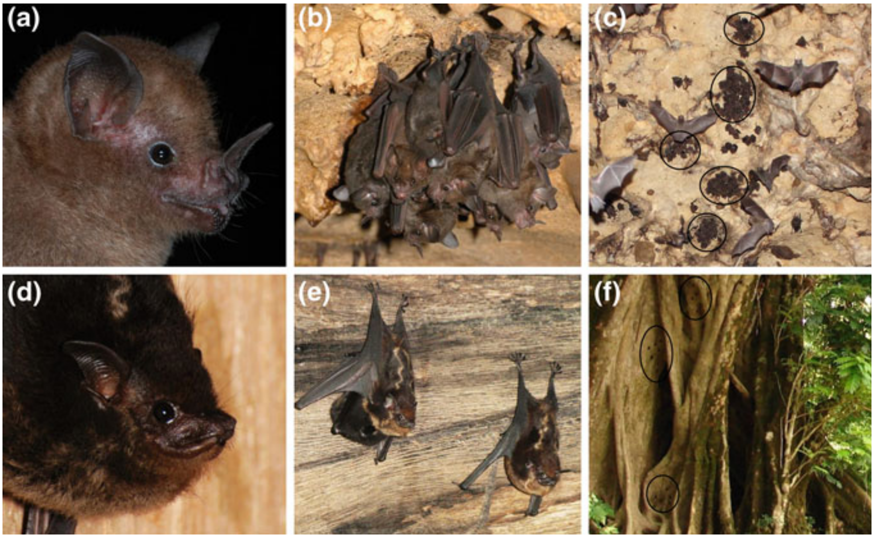

Fig. 8.1 Focal species *C. perspicillata* and *S. bilineata*. *Top panel* (*C. perspicillata*) Lateral view of head (**a**), harem group (**b**), and roosting sites of five harem groups in a mixed-species cave (**c**). *Bottom panel* (*S. bilineata*) Lateral view of head (**d**), excerpt of harem group depicting the harem male and one female with pup (**e**), and roosting sites of three harem groups on a tree (**f**). Harem groups are marked with *black circles* (**c**, **f**). *Photo credits* M. Tschapka (**a**, **b**), T. Hiller (**c**), M. Knörnschild (**d**, **e**, **f**)

8.2 Seba's Short-Tailed Bat *Carollia perspicillata*

Seba's Short-tailed Bat *C. perspicillata* is a common and widely distributed frugivoros generalist in the Neotropics (Cloutier and Thomas 1992). It is a gregarious species that often uses caves or hollow trees as day-roosts (Williams 1986; Fleming 1988; Fig. 8.1).

8.2.1 Social Organization of C. perspicillata

Male *C. perspicillata* defend roosting territories against male competitors and allow females to roost there and join their harem; thus, the mating system is a resource defense polygyny (Porter 1979a; Williams 1986; Fleming 1988). Several harem territories as well as bachelor groups, solitary bachelors, and mixed-sex subadult groups can be found in the same day-roost (Porter 1978, 1979a; Williams 1986). Compared to bachelor males, harem males are older and heavier but not always larger (Williams 1986). Harem males abandon their territories only after being displaced or when taking over a competitor's territory that is superior to their current one (i.e. has more females roosting in it; Williams 1986) and male tenure as harem holders can last up to 2 years (total tenure in all territories averages 277 days; Williams 1986). Displaced harem males sometimes establish a new territory elsewhere in the day-roost (Porter 1979a; Williams 1986). At night, harem males often return to their territories, presumably to defend them against potential intruders, whereas females and bachelor males normally do not return to the day-roost (Williams 1986). Roost site characteristics seem to be more important than male characteristics when females choose a territory to roost in (Williams 1986; Fleming 1988); however, it is unclear what females prefer exactly. Individual females rarely form long-term associations with each other and do not react aggressively toward new females joining their groups (Williams 1986; Fleming 1988). Even though males cannot prevent females from switching freely between harem territories (Porter 1979a, 1978; Williams 1986), females nevertheless spend a lot of their time (62 %) in one primary harem (Williams 1986; Fleming 1988). Harem size can be quite large (up to 18 females plus their current offspring; Williams 1986). Females can bear a single offspring twice per year and have moderately synchronized parturition within the same population (Williams 1986; Fleming 1988). Offspring dispersal from the natal colony seems to be slightly female biased; however, pups of both sexes may also remain in their natal colony, in which case they only leave their natal harem territory (Fleming 1988). Females are intensely courted by the harem males during their postpartum estrus (3–10 days after birth; Badwaik and Rasweiler 2000). Even though harem males have priority access to estrus females roosting in their territories (and thus the potential to father the females' subsequent offspring), they normally have not fathered the females' current offspring because females switched between territories in the past (Porter and McCracken 1983). Since both bachelor and neighboring harem males attempt to gain access to estrus females as well, harem males are regularly engaged in aggressive interactions with competitors (Fernandez et al. 2014).

8.2.2 *Sexually Selected Vocalizations of* C. perspicillata

The vocal repertoire of *C. perspicillata* has been described in considerable depth so far (Porter 1979b; Straub and Esser 2000; Knörnschild et al. 2013, 2014; Fernandez et al. 2014), with observations coming from captive colonies only. *C. perspicillata* produce four different vocalization types in social contexts that are under sexual selection pressure, namely territorial rival deterrence, aggressive male–male interactions, and courtship (Knörnschild 2014, Fig. 8.2, 8.3 and 8.4). These vocalization types are explained in detail below.

8.2.2.1 Territorial Rival Deterrence

At dusk and dawn, when bats are most active in the day-roost, harem males often hang from a prominent spot at the territory perimeter (e.g. from the outer rim of a

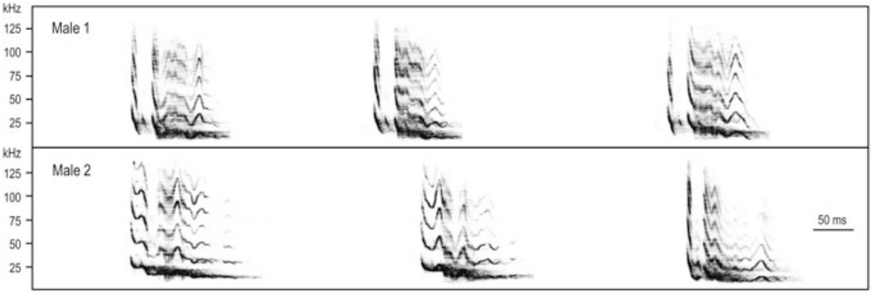

Fig. 8.2 Aggressive trills produced during territorial rival deterrence in male *C. perspicillata*. Three aggressive trills of two harem males are depicted (trills were not produced in succession but came from different recording days). This and all following spectrograms were generated using a 1024-point fast Fourier transform, a frame size of 100 %, and a Hamming window with 87.5 % overlap. All recordings of *C. perspicillata* vocalizations had a sampling rate of 300 kHz and 16 bit depth. *Recording credit* M. Knörnschild

cavity in the cave ceiling, in which the females are huddling together during the day) and produce harsh trills at irregular intervals (Knörnschild et al. 2014). These trills do not seem to be directed at a specific individual; however, trill production rate increases whenever a conspecific is flying by. We named this vocalization type “aggressive trill” (Knörnschild et al. 2014). Males most likely use aggressive trills to announce territory ownership and to deter rivals from approaching their territories. Aggressive trills are exclusively produced by males (Knörnschild et al. 2014). They contain enough interindividual variation to encode an individual signature (Fig. 8.2), and males are able to discriminate between different male rivals based on acoustic information alone (Fernandez et al. 2014). Individual discrimination of rivals likely facilitates adequate behavioral reactions between neighboring territory owners.

8.2.2.2 Aggressive Male–Male Interactions

Whenever rival deterrence based on aggressive trills is insufficient, males engage in physically aggressive interactions with competitors. During these interactions, males produce different vocalization types (Fig. 8.3), namely down-sweeps and warbles (and distress calls if they are in the inferior position). Aggressive trills often precede the actual physical contact between rivaling males, whereas warbles are mainly produced when a conflict escalates into physical contact; down-sweeps, however, are often uttered during comparatively mild disputes that are normally resolved without the opponents exchanging wing blows (Knörnschild et al. 2014). Down-sweeps and warbles are produced by both sexes, aggressive trills only by males (Porter 1979b; Knörnschild et al. 2014). In general, male–male aggressive interactions have a ritualized structure, i.e., they follow a defined succession of behavioral displays with increasing levels of aggression (Porter 1978; Fernandez et al. 2014). Boxing is a highly stereotypic behavior especially noteworthy in this

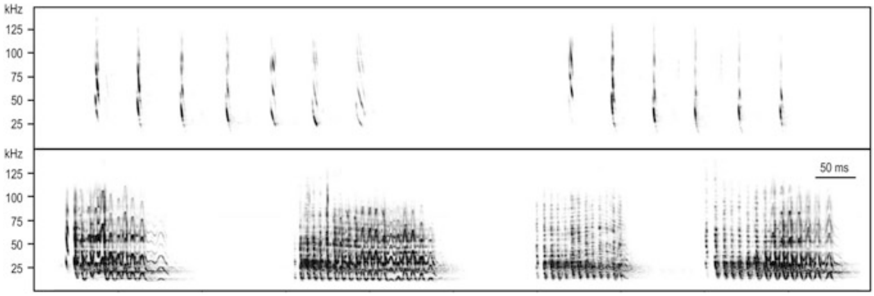

Fig. 8.3 Down-sweeps and warbles produced during aggressive interactions in male *C. perspicillata*. *Top panel* series of down-sweeps produced in succession by one male. *Bottom panel* series of warbles produced in succession by one male. *Recording credit* M. Knörnschild

context because it constitutes the top level of aggression (Fernandez et al. 2014). During boxing bouts, roosting males face one another while hanging from the ceiling of their day-roost and repeatedly distribute blows with their folded wings until one competitor retreats (Porter 1978; Fernandez et al. 2014).

8.2.2.3 Courtship

When females are estrous, harem males engage in a multimodal courtship display (Porter 1979b; Knörnschild et al. 2013, 2014). Harem males approach estrous females by brachiating or flying toward them and often briefly hover in front of them. Subsequently, they sniff the female with their body arched forward, a distinct posture that is sometimes accompanied by rapid wing beats. After sniffing, harem males repeatedly poke the female with one or both folded wings. Wing poking is the most conspicuous part of the males' courtship display, and sometimes continues for more than a minute. During copulation, males often wrap the female in both

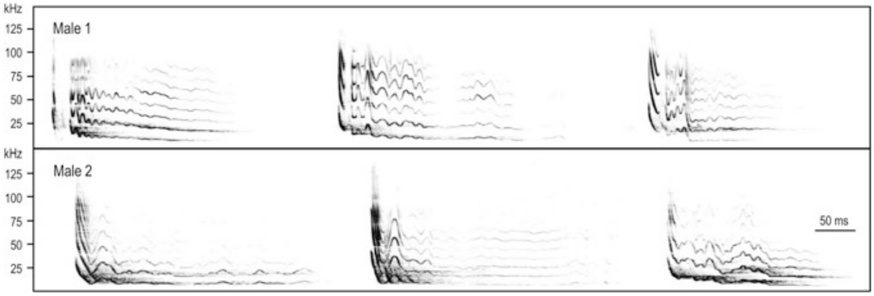

Fig. 8.4 Courtship trills produced during courtship display in male *C. perspicillata*. Three courtship trills of two harem males are depicted (trills came from different recording days). *Recording credit* M. Knörnschild

partially opened wings and apply neck bites display (Porter 1979b; Knörnschild et al. 2013, 2014). Throughout courtship (but not during copulation), males produce highly variable tonal trills at irregular intervals, which we named “courtship trills” (Fig. 8.4; Knörnschild et al. 2014). Acoustic measurements of courtship trills suggest a strong individual signature which has the potential to facilitate mate recognition or female choice (Knörnschild et al. 2014); however, a playback experiment confirming this is still lacking. A courtship trill is sometimes preceded by one or two down-sweeps (which are normally used during mild aggressive interactions; see above), especially when females elude the wing poking of males. Therefore, producing down-sweeps in addition to courtship trills might encodes the extent of male agitation (Knörnschild et al. 2014).

8.3 Greater Sac-Winged Bat *Saccopteryx bilineata*

The Greater Sac-Winged Bat *S. bilineata* is a common and widespread insectivorous bat in the lowlands of Central America (Yancey et al. 1998). It is one of the best-studied bat species worldwide with regard to its natural history, social structure, and communication system (reviewed in Voigt et al. 2008). *S. bilineata* is a very light-tolerant species that roosts on the outside of large trees, the mouths of caves, in well-lit hollow trees, or on/in man-made structures such as buildings and bridges (Fig. 8.1; Bradbury and Emmons 1974). This choice of day-roost and the fact that these bats maintain a distance of at least one body length to adult conspecifics makes it possible to observe and record individual bats with relative ease in the wild. *S. bilineata* is sexually dimorphic; males are smaller than females and have a wing-sac in each of their antebrachial membranes (Yancey et al. 1998).

8.3.1 Social Organization of S. bilineata

The mating system of *S. bilineata* is a resource-defense polygyny with single-male/multifemale groups (‘harems’). Each harem male defends a small roosting territory (approx. 1–2 m^2) in the colony’s day-roost. Neighboring territories can be directly adjacent to one another (Bradbury and Emmons 1974; Tannenbaum 1975). Normally, 2–3 adult females roost in each territory, but large harems can include up to 8 females. Average sized colonies contain 2–3 harems, but large colonies can consist of more than 10 harems (Bradbury and Vehrencamp 1976, 1977). Adult nonharem males that are queuing for territory access are also present (Heckel and von Helversen 2002; Voigt and Streich 2003), especially in large and average-sized colonies (normally 1–2 queuing males per harem). The reproductive success of harem males is much higher than that of nonharem males (Heckel and von Helversen 2002), which queue for up to 3 years to take over a newly vacant territory (Nagy et al. 2012). This normally happens when the territory owner fails to return from foraging in the morning, likely because it was predated upon. The nonharem male with the longest tenure is the first to fill in such a vacancy (Voigt and Streich 2003). However, highly aggressive territory takeovers (or attempts thereof) also occur. In this case, an intruding immigrant male (or, very rarely, a queuing non-harem male) fights with the harem male until one competitor is defeated. These fights can be severe, consisting of areal chases and collisions, biting, clawing, and hitting each other with folded wings (Tannenbaum 1975). Displaced harem males have never been observed to establish a new territory elsewhere or to remain in their colony (Tannenbaum 1975; own observations). Established harem males do not attempt to take over competitors' territories. At night, adult individuals from the same colony forage separately and do not use communal night roosts (Hoffmann et al. 2007).

Male *S. bilineata* are philopatric; thus, resident males belong to only a few patrilines (Nagy et al. 2007). Despite the high costs of local mate competition, male *S. bilineata* receive both direct and indirect fitness benefits when roosting with close kin (Nagy et al. 2012). Harem males often loose paternities to neighboring competitors (in large colonies, up to 70 % of pups are not fathered by the respective harem male; Heckel et al. 1999; Heckel and von Helversen 2003), but since resident males are normally related to many of their male neighbors, they may still gain inclusive fitness benefits. More importantly, harem male tenure (which is the best predictor of male lifetime reproductive success) is strongly and positively influenced by colony size (Nagy et al. 2012), probably because the risk of harem-takeovers by alien immigrant males is drastically reduced in colonies in which several resident males (harem and non-harem males alike) harass and may fend off the intruder simultaneously (Nagy et al. 2012).

Female choice is extremely pronounced in *S. bilineata* (Heckel and von Helversen 2003; Voigt et al. 2008). All subadult females disperse from their natal colony to avoid inbreeding with their fathers (Nagy et al. 2007) and once they are established in a new colony, they preferentially mate with genetically dissimilar males therein, and one reason for this is to avoid inbreeding with male descendants (Nagy et al. 2007). Moreover, females prefer mating partners that have a dissimilar major histocompatibility complex class I (which harbors immune genes responsible for intracellular parasite resistance; Santos et al. under review). Resident females, which often spend their entire life roosting in the same harem territory, regularly behave aggressively to each other and to dispersal females, for reasons that are currently unclear (Tannenbaum 1975, own observations). Females bear a single offspring per year and parturition is fairly synchronized (Tannenbaum 1975). Since females are larger than and physically superior to males, harem males cannot prevent females from visiting other territories in the day-roost and mating with a competitor (Heckel et al. 1999). From a female's perspective, the core social unit is likely not "harem" (as it is for the males) but "colony," because mating partners are almost always selected among the resident colony males (Heckel and von Helversen 2003). Females are in estrus for only a few days each year (Voigt and Schwarzenberger 2008), but are courted by males throughout the whole year (Behr and von Helversen 2004), which most likely reflects the large influence of female choice in this species.

8.3.2 *Sexually Selected Vocalizations of* S. bilineata

The rich vocal repertoire of *S. bilineata* has been described in great detail in the wild (Bradbury and Emmons 1974; Tannenbaum 1975; Bradbury and Vehrencamp 1976; Davidson and Wilkinson 2004; Behr and von Helversen 2004; Knörnschild et al. 2006; Knörnschild and von Helversen 2008), making it one of the best-studied bat species with regard to its social vocalizations. *S. bilineata* produce five different vocalization types in social contexts that are under sexual selection pressure (Behr and von Helversen 2004), namely territorial rival deterrence, aggressive male–male interactions, and courtship (Fig. 8.5, 8.6, 8.7). Two of these vocalizations are complex, multisyllabic songs (Behr and von Helversen 2004; Davidson and Wilkinson 2004; Behr et al. 2009). Olfactory communication plays an important role in territorial maintenance and in mate choice as well (reviewed in Voigt et al. 2008); however, only sexually selected vocalizations of *S. bilineata* are described in detail below.

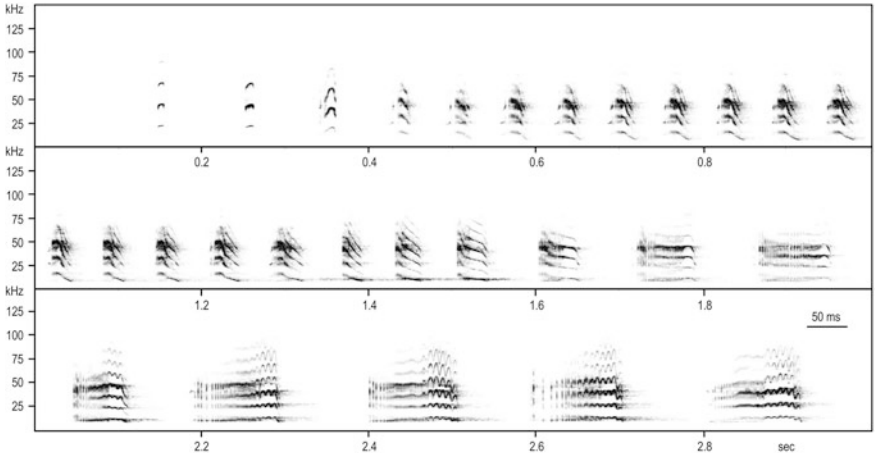

Fig. 8.5 Territorial song produced by male *S. bilineata*. This multisyllabic song starts with simple tonal syllables that gradually merge into composite end syllables (buzz syllables), which consist of a pulsed, noisy part, and a tonal part. When territorial songs precede aggressive male–male interactions, the modestly modulated tonal part of buzz syllables changes to a highly modulated trill (starting at 2.0 s). All recordings of *S. bilineata* vocalizations had a sampling rate of 500 kHz and 16 bit depth. *Recording credit* M. Knörnschild

8.3.2.1 Territorial Rival Deterrence

Harem males leave the day-roost last in the evening and return first in the morning. During these periods, they also produce the most territorial songs, both when they are alone and in reaction to conspecifics (Bradbury and Emmons 1974; Tannenbaum 1975; Behr and von Helversen 2004). Harem males utter territorial songs when male conspecifics approach the day-roost and courtship songs (see below) when females approach the day-roost (Knörnschild et al. 2012). Territorial songs are multisyllabic vocalizations. They start with simple tonal syllables that gradually merge into composite end syllables ('buzz syllables') consisting of a harsh, pulsed part, and a tonal part (Fig. 8.5). Territorial songs are comparatively long (on average 1.6 s, maximum 4 s) and low in frequency (on average 14.5 kHz, minimum 7 kHz; peak frequency of buzz syllables was measured), making them unusual bat vocalizations (Behr et al. 2006, 2009). Adult females do not produce territorial songs (Behr and von Helversen 2004). Male reproductive success is positively correlated with song rate and negatively correlated with song peak frequency (Behr et al. 2006). Harem males respond more aggressively to broadcast territorial songs with a lower peak frequency than to songs with a higher peak frequency (Behr et al. 2009), indicating that the former are perceived as a greater threat. Male song rate is positively correlated with the number of male competitors and the number of harem females (Davidson and Wilkinson 2004; Behr et al. 2009; Eckenweber and Knörnschild 2013), suggesting that male singing augments with increasing male–male competition. The buzz syllables of territorial songs (which are equivalent to the screech-inverted-V call type described in Davidson and Wilkinson 2002; 2004; pers. comm. G. Wilkinson) contain enough interindividual information to encode an individual signature (Davidson and Wilkinson 2002, Eckenweber and Knörnschild 2003). Moreover, buzz syllables from colonies within hearing range of each other encode a group signature (Eckenweber and Knörnschild 2003) and, over a larger geographic scale, buzz syllables show regional variation (Davidson and Wilkinson 2002). However, playback experiments confirming that *S. bilineata* actually uses those signatures are still lacking. Since territorial songs are not innate but learned by imitating tutor males during ontogeny (Knörnschild et al. 2010b; Knörnschild 2014), it is currently unclear whether group signatures and regional differences are caused by learning processes or genetic effects (i.e. because philopatric, related males sing similarly). Despite the fact that territorial songs are used to mediate territorial claims among males, it is conceivable that they can also be directed at females. The above-mentioned correlation between male reproductive success on the one hand and song rate and peak frequency on the other hand (Behr et al. 2006) does not allow us to infer whether territorial songs advertise the competitive ability of males (a signal directed at other males) or the quality of territory holders (a signal directed at females); of course, both options are not mutually exclusive.

8.3.2.2 Aggressive Male–Male Interactions

Aggressive interactions between males involving physical contact are rare in *S. bilineata*, but when they occur they are severe (Tannenbaum 1975; Behr and von Helversen 2004; own observations). Territorial songs (and scent-marking at territory borders; Voigt and von Helversen 1999; Caspers and Voigt 2009) are normally sufficient to keep male rivals at bay, but once territory ownership is challenged, harem males react most aggressively. Territorial songs often precede aggressive male–male interactions (Tannenbaum 1975; Behr and von Helversen 2004; own observations); in this case, the tonal part of buzz syllables changes from its normal modest frequency modulation to a highly modulated trill, while the pulsed part remains unchanged or decreases in length (Eckenweber and Knörnschild 2013, own observations; see also Fig. 8.5). During physically aggressive interactions, males produce three different vocalization types (Fig. 8.6), namely barks, screeches, and pulsed trains (and, if they are inferior, also distress calls; Behr and von Helversen 2004; own observations). Pulsed trains are somewhat similar to buzz syllables of territorial songs, but the former are produced singly, not in succession and their harsh, pulsed part is greatly enhanced when compared to buzz syllables (however, a short tonal part is sometimes present at the end of pulsed trains as well). Screeches and pulsed trains are mainly produced when a conflict escalates; barks, however, are often uttered during comparatively mild disputes, or, like territorial songs, before the onset of a dispute (Behr and von Helversen 2004; own observations). Screeches, barks, and pulsed trains can be produced by both sexes, but males utter much more barks and pulsed trains than females (own observations).

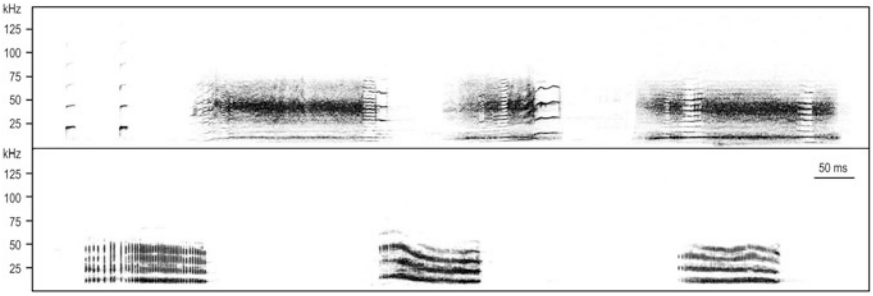

Fig. 8.6 Barks, screeches, and pulsed trains produced during aggressive interactions in male *S. bilineata*. *Top panel* two barks produced in succession by one male and three screeches (from different males; not produced in succession). *Bottom panel* Three pulsed trains, reminiscent of buzz syllables in territorial songs, from different males (not produced in succession) *Recording credit* M. Knörnschild

8.3.2.3 Courtship

Males court females everyday throughout the whole year with conspicuous and multimodal courtship displays that consist of visual, olfactory, and acoustical components (Bradbury and Emmons 1974; Tannenbaum 1975; Bradbury and Vehrencamp 1976; Voigt and von Helversen 1999; Behr and von Helversen 2004; Davidson and Wilkinson 2004). Males court females mostly when they return to their harem territory at dawn, and, to a lesser extent, before they leave it at dusk (Behr and von Helversen 2004). Male courtship is most intense during the mating season and continues at lower levels thought the rest of the year (Tannenbaum 1975; Behr and von Helversen 2004). The most conspicuous aspect of male courtship is a hover display during which a male hovers in front of a roosting female while presenting olfactory signals from the wing-sacs (Voigt and von Helversen 1999) and vocalizations (Behr and von Helversen 2004; Davidson and Wilkinson 2004). Hovering males produce long whistles to which females often respond with screeches in a

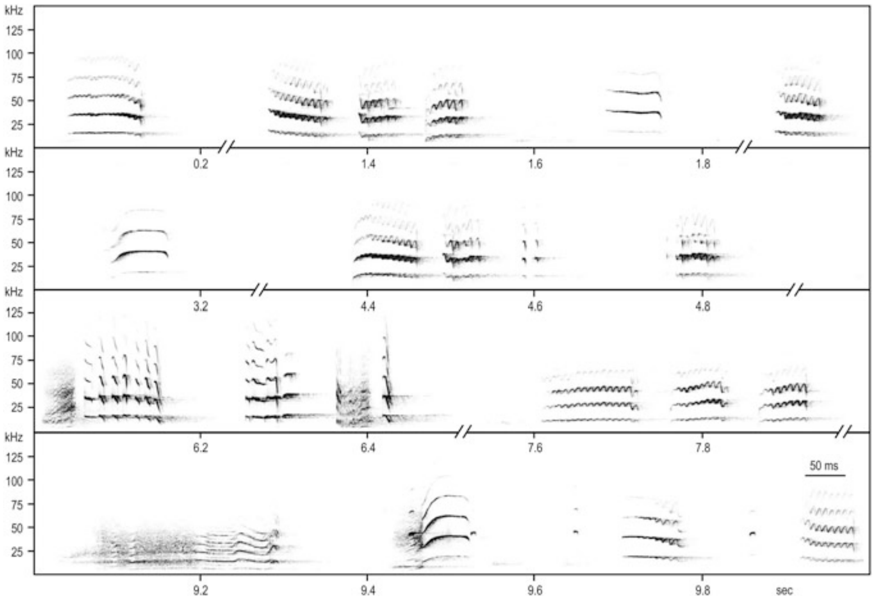

Fig. 8.7 Courtship song produced by male *S. bilineata*. Courtship song excerpt from one harem male, depicting different trill types, long tonal calls, noise bursts, and a whistle. The excerpt ends with a hover display: the female's screech (9.0–9.3 s) is followed by the male's whistle (9.4–9.5 s) and two trills (9.7–10.0 s). The screech (9.0–9.3 s) and four echolocation calls (9.4–9.9 s) were produced by the female, all other vocalizations by the male. Please note that several silent parts (of approx. 1 s each) are not depicted in the spectrogram *Recording credit* M. Eckenweber

duet-like way (Behr and von Helversen 2004; own observations). Copulations are normally preceded by male hover displays (Tannenbaum 1975; own observations), so they seem to be crucial for females to assess male quality. Male hover displays are embedded in long courtship songs during which the male approaches a roosting female from different angles by short flights and crawling (Behr and von Helversen 2004). This male approach behavior, accompanied by conspicuous head turns toward the courted female, is always associated with the production of courtship songs; when it ends, song production ceases as well (Behr and von Helversen 2004). In the mating season, courtship attempts (and thus courtship songs) directed at one particular female that can last for up to one hour, but most courtship songs are much shorter (on average 42 s; Behr and von Helversen 2004). Courtship songs consist of different syllables types, with purely tonal trills being the most common one (Fig. 8.7). Trills are highly variable, and males differ in their trill repertoire (Behr and von Helversen 2004), suggesting that females might use trills for mate choice decisions; however, a playback experiment confirming this is still lacking. When not interested in male courtship attempts, females do not evade them but terminate them aggressively (Tannenbaum 1975; Behr and von Helversen 2004).

8.4 Synopsis

Despite the fact that both *S. bilineata* and *C. perspicillata* exhibit resource-defense polygyny and live in single-male/multifemale groups, their social organizations seem to differ remarkably in certain aspects, e.g., the way resident harem males interact with each other or the amount of female choice involved in mating (see Table 8.1 for an overview of key differences between both species). It is conceivable that these differences have implications for the structural complexity and information content of sexually selected vocalizations.

When considering vocalizations used in the context of territoriality or aggression, we find obvious differences in vocal complexity and associated behaviors between both species. Male *S. bilineata* produce long, structured territorial songs encoding information about male quality, identity, and group membership (Davidson and Wilkinson 2002, 2004; Behr et al. 2006, 2009; Eckenweber and Knörnschild 2013) which, together with scent marking (Voigt and von Helversen 1999; Caspers and Voigt 2009), is often enough to keep male rivals at bay. When disputes cannot be solved from a distance by singing and scenting, the resulting physically aggressive conflicts are severe and do not follow a ritualized structure (Tannenbaum 1975, own observations). This contrasts sharply with the ritualized aggressive interactions between male *C. perspicillata*, in which a defined succession of behavioral displays with increasing levels of aggression mediates conflicts (Porter 1978; Fernandez et al. 2014). Physically aggressive interactions between males are much more common in *C. perspicillata* than in *S. bilineata* throughout the year. This is probably caused by the fact that *C. perspicillata* bachelor males do not queue for territory access and that resident harem males fight among each other

Table 8.1 Key characteristics of social organization and behavioral interactions in *S. bilineata* and *C. perspicillata*

Characteristics	*Saccopteryx bilineata*	*Carollia perspicillata*
Mating system	Resource-defense polygyny	Resource-defense polygyny
Social structure	One-male/multifemale groups (harems) with bachelor males (single)	One-male/multifemale groups (harems) with bachelor males (single or in groups)
Colony structure	Often several harems (up to 12)	Often several harems (up to 18)
Roosting behavior	Adults roost at least one body length away from conspecifics	Adults roost with body contact
Sexual dimorphism	Males are approximately 15 % smaller than females; only males have wing-sacs	In most areas, males are heavier but not larger than females
Harem size	Up to 8 females	Up to 18 females
Average tenure as harem male	On average 1.9 years (up to 9 years)	On average 0.8 years (up to 2 years)
Territorial scent marking by males	Yes	No
Superior sex in aggressive interactions	Females	Males
Male-male aggression	Acoustical and olfactory rival deterrence is very common, physical conflicts are rare but severe	Acoustical rival deterrence is very common, physical conflicts are common but normally not severe
Female–female aggression	Prominent	Rare
Multimodality of male courtship display	Acoustical, olfactory, visual	Acoustical, tactile, olfactory (?)
Vocal response of females to male courtship	Yes	No
Female estrus	One seasonal estrus	One postpartum estrus and one seasonal estrus
Parturition	Fairly synchronized (within 2–3 weeks)	Moderately synchronized (within 6–8 weeks)

for the territories most preferred by females (Williams 1986; Fleming 1988). Thus, it is not surprising that male *C. perspicillata* use comparatively simple vocalizations, aggressive trills, to announce territory ownership but resort to a comparatively more advanced suite of ritualized behavioral displays to resolve the numerous physically aggressive conflicts than *S. bilineata* males.

We also find strong differences in vocal complexity and accompanying behaviors between both species when considering vocalizations used in the context of courtship. Male *S. bilineata* produce extremely long courtship songs, which incorporate sophisticated hover displays in which males and females often interact with each other in a duet-like fashion (Behr and von Helversen 2004). In contrast to the elaborate, year-round courtship of *S. bilineata* males (which also has an important olfactory component; reviewed in Voigt et al. 2008), male *C. perspicillata* produce single courtship trills in succession while following an estrous female on foot in their harem territory until the female consents to mating (Porter 1979a; Knörnschild 2014). This obvious difference in male courtship behavior may be caused by two factors: First, female choice might be more pronounced in *S. bilineata* than in *C. perspicillata* because, in the former species, females are larger and thus physically superior to males (Yancey et al. 1998). Second, ownership of a territory that is particularly preferred by females (and thus heavily fought for among males) is already a strong indicator of male quality in *C. perspicillata*, which may explain why courtship in *C. perspicillata* is less elaborate than in *S. bilineata*. Female *S. bilineata* do not obviously prefer a specific male territory, probably because their roosting associations within a colony are not automatically determining their mating partners (Heckel et al. 1999; Heckel and von Helversen 2003). Instead, female *S. bilineata* can evaluate all resident males in a colony throughout the whole year and make their yearly mate choice decisions accordingly, which may have led to the complex courtship displays of male *S. bilineata*.

In conclusion, *S. bilineata* seem to have more complex territorial and courtship vocalizations than *C. perspicillata* because male *S. bilineata* try to resolve territorial disputes without physical aggression and because female choice is extremely pronounced, driving males to court females year-round. Thus, not only the strength of sexual selection pressures (which can be hard to assess), but the details of a species' social organization and behavioral interactions can influence the structural complexity and information content of sexually selected vocalizations in bats.

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Chapter 9

Daily and Seasonal Patterns of Singing by the Mexican Free-Tailed Bat, *Tadarida brasiliensis*

Michael Smotherman, Kirsten Bohn, Kaylee Davis, Kelly Rogers and Christine P. Schwartz

Abstract Singing is a specialized vocal behavior that supports courtship and territoriality but costs energy and time. Singing behaviors are well documented in the Mexican free-tailed bat, *Tadarida brasiliensis*, but many important questions about the functional significance of singing in this species remain unanswered. To better understand how singing benefits this species we analyzed daily and seasonal temporal patterns of singing in both a natural and a captive colony for extended periods of time and measured the average call and song rates over the course of seven days and over one entire year. Analyses revealed that under natural conditions singing was most prevalent at onset of the spring and fall migration periods but also continued at a less frequent rate throughout the summer months. Singing rates were highest during the spring mating season, but singing also continued through the summer months in exclusively male colonies. In a natural roost, males sang the most just before sunrise, but also sang prolifically just after sunset and sporadically throughout the night. This pattern suggested that singing patterns were driven by the activity of conspecifics leaving and returning to the roost, and also indicated that singers may spend less time foraging than their roost-mates. We tested this by measuring movements and singing patterns in a captive colony, where roost-mates were confined to flying around the vivarium at night. Under these conditions captive bats sang continuously at high rates throughout the night. We propose that singing by *T. brasiliensis* evolved initially to facilitate migration by facilitating more rapid localization of roosts by bats passing through novel territories, particularly just before sunrise. Singers sacrifice foraging time but may

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gain a reproductive advantage by attracting more bats to their roost during the spring mating season, which may explain why males but not females of this species sing.

9.1 Introduction

Male *Tadarida brasiliensis* sing a complex multisyllabic song from perches within their day roosts (Bohn et al. 2008, 2009). These songs are suspected of serving both courtship and territorial defense functions, alerting and attracting females to the presence and location of the singers' roosts and presumably dissuading competing males from entering the roost (Bohn et al. 2013). However, many aspects of the free-tailed bat's singing behavior are inconsistent with this simple explanation. The current interpretation of the behavior is largely based on similar examples from songbirds, but whether bats use song the same way and for the same reasons songbirds do is uncertain (Catchpole and Slater 2008). Singing has been documented in at least a dozen species of bats, including members of the families Vespertillionidae (Barlow and Jones 1997; Jahelková et al. 2008; Sachteleben and von Helversen 2006; Zagmajster 2003), Emballonuridae (Behr and von Helversen 2004; Davidson and Wilkinson 2004), Megadermatidae (Leippert 1994; Mcwilliam 1987; Schmidt 2013; Vaughan 1976; Vaughan and Vaughan 1986), and Molossidae (Bohn et al. 2009, 2013). Many interesting similarities in the ways bats and birds use songs to defend foraging territories and attract mates can be found among these examples, but significant differences in the reproductive and foraging ecology of these two large and diverse taxa make it unlikely that singing serves identical functions in both bats and birds. For example, songbirds generally sing to establish and defend an exclusive home territory that accommodates both foraging and mating needs, whereas most bat species utilize separate foraging and roosting sites. Also, whereas songbirds routinely integrate visual displays into their repertoires bats may be expected to rely more heavily on acoustic signaling for a wider array of their social behaviors, such as group cohesion and maintaining social hierarchies.

Like many bat species (Kunz and Lumsden 2003), adult male and female *T. brasiliensis* roost separately for most of the year; females form large maternity roosts in the spring and early summer while males spread out across the countryside, transiently forming small-to medium-sized groups along their migration routes (Best and Geluso 2003; Davis et al. 1962). Small mixed-sex roosts are also found, but these appear most often during the spring and fall migratory seasons. Few details are known about *Tadarida*'*s* mating behavior, and despite detailed studies of the singing behavior, it remains to be shown whether song influences female mating preferences or if any form of sexual selection occurs in this species. Only a small percentage of adult males sing at any one time, but there is no information available to explain why some males sing and others do not. Furthermore, although under some circumstances singing males will forcibly evict intruder males (Bohn et al. 2013; Schwartz et al. 2007), it is common for singing males to share roosts with other nonsinging males, again suggesting that singing plays a subtler role in *Tadarida*'*s* sociality than is currently understood. Thus, definitive evidence of the free-tailed bat song's function and ecological significance is lacking. One way to address this issue is to directly measure when male bats sing. Among songbirds, daily and seasonal patterns of singing coincide with migratory, foraging and mating behaviors, thereby providing circumstantial evidence of a song's function for a given species (Marler and Slabberkoorn 2004). Here we provide a description of daily and seasonal patterns of singing in a year-round natural roost-site and also in a captive colony of bats. The results suggest that songs may have many functions including a general role in roost localization, conspecific recognition, group cohesion, and possible mate selection. In mating contexts, singing likely gives a male a reproductive advantage by increasing immediate access to females, whether or not any song parameters directly influence female choice.

9.2 Methods

9.2.1 Study Site and Animals

Field recordings were conducted at designated roosting sites within and around the University football stadium (Kyle field), which housed a year-round colony of *T. brasiliensis* that varied in size from roughly 50,000 individuals in the winter months to more than 250,000 during the spring (March) and fall (October) migratory seasons. Within the stadium, small groups of bats that were reliably located in easily accessible places were videotaped and their vocalizations recorded once a week in the late afternoon from January 2006 to January 2007. Additional recordings and observations were made at four–six different times of the year from 2007 to 2012. Over this six-year period a total of 750 bats were captured in groups of 20–30 at a time at different times of the year, and their sex, weight, and forearm lengths were documented. Of these, 92 % were male, and females were only captured during March and October. However, on the rare occasions that females were encountered, they were captured in small groups composed almost exclusively of females, suggesting that the females were traveling and roosting together during their migration. Only males were found overwintering in the stadium, and the most preferred roosting sites within the stadium were never found completely abandoned. The primary roost-site used for this study (Fig. 9.1) was a 5 cm high, 20 cm deep, and 5 m long concrete expansion joint (or crevice) chosen because it housed bats continuously all year and because the group size was small enough (20–100 bats) that the songs of individual bats could be discriminated from the din of the colony. Singers comprised only about 5–10 % of the group and they were spatially distributed among the population. In 2013, the colony was forcibly expelled from the stadium and excluded by netting prior to the structure's demolition and renovation.

Fig. 9.1 Tightly packed Mexican free-tailed bats roosting in a concrete expansion joint within the Texas A&M football stadium (Kyle field), College Station, Texas, USA

For field investigations of daily singing patterns we recorded continuously at the target roost-site 24 h a day for seven days (April 10–17, 2010). To study singing in the laboratory, we maintained a colony of bats in the biology department vivarium in a room large enough to allow free flight (4 × 10 × 3 m). The room had regulated light–dark cycles adjusted with a light timer to mimic the natural durations of the external photoperiod except that the artificial sunset was shifted to coincide with 12:00 pm to facilitate morning feedings, cleaning, and maintenance, and was temperature and humidity controlled. Bats were roosted in artificially constructed bat houses (Maberry Bat Centre, Daingerfield TX) within the room and were fed by placing bowls of meal worms (*Tenebrio* larvae) on feeding platforms hanging on the walls. Typically, bats emerged from the artificial roost house 30–60 min after the lights went out, flew around the room for 15–30 min, and then landed on the platform to feed. Bats would then alternate between bouts of flying, eating, and resting throughout the night and return to the roost house shortly before the light was activated. The room was cleaned daily and fresh food and water were placed on the feeding platform during the past hour of the lighted period to minimize disturbing the bats during their most active periods. For 24-hour recordings, the time of day is presented relative to sunset or lights off, also known as zeitgeber time 12:00 (ZT 12) following the standard notation for circadian rhythms of nocturnal animals. All experiments were reviewed and approved by the Texas A&M Institutional Animal Care and Use Committee.

9.2.2 Acoustic Recordings

All vocalizations were recorded using an externally polarized condenser microphone (Avisoft Bioacoustics, Berlin Germany, model CM16) and digitized at 12-bit/250 kHz sampling rate using the Avisoft Ultrasound Gate model 116 for storage on a personal computer running the Avisoft-Recorder software (v. 2.9). For field studies, the microphone was positioned on a tripod approximately 3 m from and oriented toward the target roost-site. Other small colonies located in nearby crevices were within range of the microphone, but vocalizations emanating from these neighboring colonies were excluded from analyses because their peak amplitudes fell below the minimum voltage threshold used for extracting pulses, calls, and songs emanating from the target roost-site; on-axis signals of interest were at least 20 dB greater than off-axis background noise. For vivarium studies, the microphone was placed 1 m below the artificial bat house in which the bats roosted, and positioned off-center just far enough so as not to impede access to or emergence from the roost. The microphone was able to record all vocalizations in the room, but songs emanating from the bat house were distinguishable from other sounds based on their acoustic features (relative loudness, spectrotemporal metrics, and echo reverberation patterns).

For analyses we included all songs that were of sufficient quality for measurements and syllable identification (see Bohn et al. 2009 for details). "Songs" were defined as discreet sequences of a unique set of syllables and phrases (chirps, trills, and buzzes) that followed a stereotyped phonological syntactical pattern previously characterized as typical of singing in this species (Bohn et al. 2009). Individual males sing multiple song types and variants, which were all lumped together for this analysis, and songs were often sung in bouts, wherein songs were produced at high rates (20–30 per minute) for short periods of time (20–30 s). Bouts were separated by periods of silence that varied in duration depending on the activity levels of nearby conspecifics. Biosonar pulses, calls, and songs were extracted and their acoustic parameters were measured using Avisoft SASlab v.4.9 and SIGNAL v.4 (Engineering Design, Cambridge MA). We used bout analyses on the intervals between syllables to objectively cut bouts into individual songs. We used oscillograms and spectrograms to identify phrases within songs and syllables within phrases. "Calls" were defined as any other non-biosonar vocalizations, including various protest calls, herding calls, begging calls, and any trills or buzzes not uttered as part of a song. Since wild colony sizes were constantly in flux and activity levels varied from day to day and with ambient temperature, we measured total and mean call rates to provide a relative estimate of the numbers of animals within the crevice during each recording session. For further technical details about the acoustic analyses please refer to Bohn et al. (2009, 2013).

9.3 Results

9.3.1 Seasonal Variations in Song Production

During the six-year period of this study it was typical for large groups of *T. brasiliensis* to begin arriving at the stadium during the last week of March and again during late September. No other species of bat was detected roosting in the stadium. The peak colony size was estimated to be 140,00–280,000 bats based on measures of local population densities (250–500 bats per square meter) and the calculated total used roosting space (≈560 m^2 of concrete expansion joints and other crevices). During the intervening summer months the colony size varied substantially from year to year, but was consistently smaller than during the migratory periods. A smaller population continued to roost throughout the winter months, although the colony size was at its lowest during the coldest periods of the year. It was also observed that group sizes within different cracks and crevices varied daily and weekly throughout the year, suggesting that individual bats did not necessarily return to the same roost within the stadium each night. Although it was not logistically feasible to count population numbers at the natural roosting site, it was assumed that average call rate at the recording site should correlate weakly with population density and activity levels, and therefore might provide some insight into any major patterns of change in group size across seasons. Mean call rates varied from 0 to 200 calls per minute at the site, and call rates changed seasonally in a manner consistent with estimates of seasonal changes in the population density (Fig. 9.2a). Since songs made up approximately 1–2 % of total vocalizations, to facilitate comparisons call rates were plotted as "per minute" while song rates were plotted "per hour" to facilitate comparisons of temporal patterning. Calling and singing rates increased in March coincident with the beginning of the northward spring migratory period, and singing rate peaked in May while calling rate peaked in June (Fig. 9.2a). Calling and singing rates both declined in July only to rise again in August. Calling rates were elevated throughout October, which corresponded with the arrival of southward migrating bats, but singing declined sharply from August to October. Although calling from the roost was documented every month of the year, no singing was recorded during the months of November through February. The highest relative song rate (percentage of vocalizations that were songs) was recorded in March and singing rates systematically declined from April until August (Fig. 9.2b). Interestingly, however, relative song rate peaked again in August to a level nearly as high as was recorded in March. Singing rates were not positively correlated with call rate but did appear to be closely associated with the timing of seasonal migration patterns.

In the natural roost several natural parameters were changing daily and seasonally that could not be controlled for but were assumed to influence calling and singing rates. It was not feasible to directly measure population size, so we used mean call rates to estimate relative changes in population density. Daily activity levels were sensitive to ambient temperature, thus mean call rates reflected a nonlinear interaction between population density and temperature-dependent activity levels within the roost. This relationship arises because the majority of social calls emanating from the roost are protest calls elicited by bats pushing and shoving each other as they move about the roost. In order to better predict the relationship between calling rates, activity levels, and group sizes, we examined the effects of daily temperature on calling and singing rates. Activity levels of free-tailed bats within the roost are sensitive to ambient temperatures, and calling rates are influenced by activity levels. Thus, we predicted that calling rates should display a positive correlation with temperature. Daily temperature records were obtained from a nearby airport (Easterwood Airport, College Station, TX; the

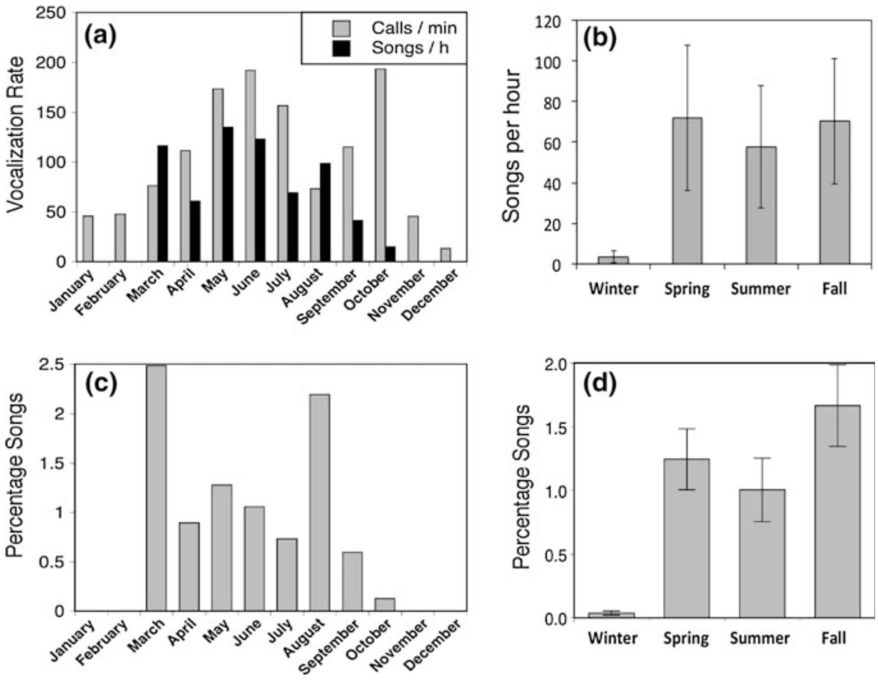

Fig. 9.2 Seasonal patterns of Mexican free-tailed bat song emissions from a natural roost in College Station, Texas, USA. **a** Monthly calling and singing rates were measured by pooling the total numbers of all calls and all songs extracted from weekly recording sessions and dividing by the total length of recording. Note that calls are given per minute whereas songs are given per hour because calls were much more frequent and included all types of calls (see Bohn et al. 2008 for description of call types). **b** Song rate varied with seasonal migration ($F_{3,39} = 3.1$, $p = 0.04$). Winter = October–February, Spring = March–May when females migrate northward, Summer = June–July and Fall = August–September, when females migrate southward. **c** Songs as a percentage of all social calls recorded per month. **d** The percentage of all vocalizations (songs and calls) that were songs varied with season migration ($F_{3,39} = 6.6$, $p = 0.001$). Winter = October–February, Spring = March–May when females migrate northward, Summer = June–July and Fall = August–September, when females migrate southward

airport is on the Texas A&M campus and approximately 1 km from the stadium) and we examined the relationship between peak daily temperatures, calling rates and singing rates (Fig. 9.3a). Peak temperature fluctuated from 50 to 95 degrees Fahrenheit, with highs in July and August and lows in November and December. Beyond the observation that singing only occurred in the spring and summer months, no clear correlation between singing and calling was apparent. However, a correlation was revealed in Fig. 9.3b, which plots song and call rates versus the peak temperatures on the day of recordings. Both call and song rates were positively correlated with temperature (Spearman rank order; $P = 0.532$, $p < 0.001$ and $P = 0.601$, $p < 0.001$, respectively). For both, the relationship could be modeled by a common single exponential growth function (rate = $e^{0.05*T}$, $p \leq 0.001$ for each),

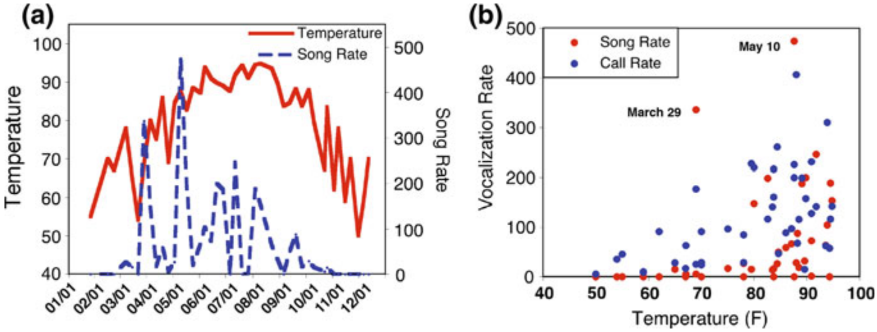

Fig. 9.3 Temperature effects on Mexican free-tailed bat vocalization rates in College Station, Texas, USA. **a** Weekly records of singing rates (per hour) and peak temperatures are plotted for the days of each recording. **b** Plot of the mean calling and singing rates versus peak temperatures. Dates are provided for the two days with the highest recorded singing rates (March 29th and May 10th)

suggesting that the relationship between activity levels within the roost and recorded calling rates is predictable. However, some important differences in the relationship between temperature and calling versus singing were also evident. In particular, with one important exception singing only occurred at temperatures above 75 °F, whereas calls were recorded across the entire temperature range. Also, after accounting for the correlation between temperature and singing, it appears that the highest recorded singing rate occurred earlier in the spring and at a lower temperature than what would have been predicted if singing was constrained by ambient temperature alone. In consideration of these observations we conclude that the burst of singing that occurs in the spring was not due solely to increased ambient temperatures.

9.3.2 Daily Patterns of Song Production

To determine when during the daily cycle bats were most likely to sing, we analyzed 7 consecutive days of continuous recordings from the natural roost-site and from within our bat vivarium. At the natural roost (Fig. 9.4a), singing rates rose sharply during the first two hours after sunset and then dropped back down to a lower rate that was sustained throughout the night. Song rates peaked again to their highest levels during the two hours preceding sunrise. This pattern is consistent with our previous observations (Bohn et al. 2013) that although some singing is spontaneous, hearing the echolocation pulse emissions of bats flying past the roost is the most potent cue for evoking singing. Our interpretation of Fig. 9.4a is that bats sang most robustly when hearing bats exiting the roost after sunset and again when they heard bats return to the roost before sunrise. The observation that at least some bats remained at the roost for most of the night and continued to sing

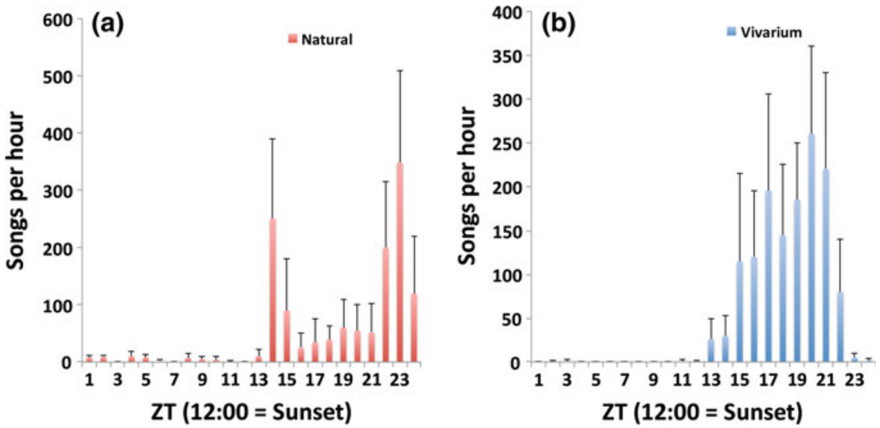

Fig. 9.4 Daily singing patterns of Mexican free-tailed bats in a natural and an artificial roost in College Station, Texas, USA. Graphs show the average number of songs per hour over a seven-day period in a natural roost (**a**) (April 10–17, 2010), and the pooled data sets from three different bats recorded for seven consecutive days in the vivarium (**b**) (April 21–28, 2010; May 5–14, 2011; March 27–May 5, 2012). Under both conditions peak singing rates occurred in the hours just before sunrise. Hours are given in Zeitgeber time, with 12:00 set equal to sunset (natural roost) or lights off (vivarium)

sporadically was surprising. All bats must leave the roost at some time each night to feed, thus it is likely that the sustained nighttime singing reflects the comings and goings of bats throughout the night. As mentioned above, there was usually more than one singing bat present at the roost, but we had no way of tracking the location and identity of individuals or determining when and for how long individual singers may have left the roost.

Support for the hypothesis that circadian rhythms in singing were triggered by circadian rhythms in the activity patterns of other bats (i.e. hearing the pulse emissions of other bats) is further supported by comparing daily singing rhythms in our vivarium. In the vivarium, bats do not leave for the night as in the wild and thus we predicted that singing would be higher throughout the night as bats took flight within the confined space of the vivarium. Data from three individuals, each recorded continuously for a 7-day period, supported this. Although singing rates rose rapidly in the first two hours after sunset (lights off) as in the wild, singing rates remained elevated throughout the night. Singing receded earlier in captivity than the wild—two hours preceding sunrise (lights on). This may reflect a pattern of bats returning to their artificial roost-sites within the vivarium before sunrise once they had eaten all of the available food. As bats returned to the day roost sonar pulse emissions during flight receded and consequently the singing stopped. During these experiments we visually confirmed that the singing bats periodically left the artificial roost for brief periods to eat at the feeding station. Importantly, we observed that the singers could still be provoked to sing even while eating at the feeding station.

9.4 Discussion

Male free-tailed bats produce the most songs from within their roost during the past few hours before sunrise when conspecifics are returning to the day roost, but they also sang prolifically in the evening while bats were leaving the roost. We also found that singing from the roost continued throughout the night, indicating that under natural conditions a roost-site was never left unattended by at least one singing male. This may reflect a pattern of singing males making many short foraging trips and return frequently to guard the roost against intruding males, or it may be that singing males take turns foraging while others remain at the roost. Finally, our investigation of seasonal singing behavior found that singing was most prevalent in early spring during the time period when many bats are migrating northward to temperate feeding grounds (Best and Geluso 2003; Gillam and McCracken 2007; Horn and Kunz 2008). Importantly, singing continued throughout the summer months during times when females were scarce. During this time female *T. brasiliensis* aggregate to form nursery colonies in select large caves throughout the southwest United States (Davis et al. 1962; Gelfand and McCracken 1986). We also found evidence that a second peak in the relative frequency of singing occurred in late August, which just preceded the beginning of the southward fall migration period.

We have previously hypothesized that the primary function of the song appears to be to alert passing bats, especially females, to the presence and location of a suitable day roost (Bohn et al. 2013). This was based on three key pieces of evidence: first that singing is rapidly triggered by the echolocation pulses of bats flying past the roost entrance, second that singing is a sexually dimorphic behavior performed by males, and third that singing males are known to aggressively expel unwelcome males from their roost-site (Bohn et al. 2013). However, the observations reported here indicate that singing may serve a broader ecological function than just sexual selection, namely group cohesion. Free-tailed bats form some of the largest, densest colonies of mammals on the planet, and singing may play a pivotal role in maintaining these groups and more generally in how migrating bats manage to locate safe day roosts before sunrise each morning. The fact that singing males routinely shared their densely crowded day roosts with many other males and continue to singing throughout the summer months in the absence of females argues against the song's sole purpose being to attract mates and repel competing males. Singing appears to be most strongly affiliated with the spring migration, which supports the hypothesis that singing may indirectly enhance a male's reproductive success by increasing access to females. It is believed that mating occurs during the early spring and that the pregnant females thereafter aggregate to form nursing colonies, giving birth in early June and weaning the pups by mid-July (Kunz et al. 1995; McCracken 1984). Not all nursery colonies are in large caves, however, as substantially large nursing colonies have also been found in artificial structures such as bridges in San Antonio, Austin, and Houston, Texas. Females were rare at the stadium in College Station, however, and year after year were only encountered during brief periods in the spring and fall. Thus, it seems reasonable to speculate that singing is likely to attract females to the singer's roost during the mating period in springtime but may also serve another function outside of mating season. Singing may serve in maintaining group cohesion and possibly facilitating migration again in the fall, independent of any reproductive benefits.

One of the more thought-provoking aspects of our long-term observations was that only 5–10 % of the adult male free-tailed bats in a roost sing, and those bats appeared to space themselves out among the many available roost-sites throughout the stadium. We do not know why all male bats do not sing or what the social or environmental cues may be that are responsible for initiating singing by one individual but not others. During ten years of observations in our captive colony we have rarely observed more than one bat at a time singing in the colony. When the singing male was removed or simply stopped singing, another male soon replaced it as colony singer. This would seem to suggest that one male's singing may inhibit the behavior in other males in the colony, and that loss or removal of this inhibitory stimulus somehow allows or motivates another male to begin singing, but this remains to be tested. If this were the case it would be consistent with the hypothesis that singing serves an important general function for group cohesion and maintenance in addition to any reproductive advantages afforded the singer. It might then follow that singing first evolved in *T. brasiliensis* in support of migratory behaviors by helping bats in transit quickly find suitable day roosts when passing through foreign territory, and subsequently became integrated with mating behaviors because singers gained better access to migrating females in the spring. It should be emphasized here that currently there is as yet no direct evidence that singing by male *T. brasiliensis* directly influences female mate choice preferences. However, singing has been shown to guide female mate choice in the sac-winged bat *Saccopteryx bilineata* (Behr et al. 2006), so further experiments to test this possibility in *T. brasiliensis* appear justified.

It also is unclear why the bats sang shortly after sunset, a time when their roost-mates were leaving rather than returning to the roost. Singing is energetically costly and so its occurrence at sunset should provide some benefit that outweighs both the metabolic costs and the loss of foraging time and opportunities, but the nature of this benefit remains obscure. It is possible that sunset singing arises as a necessary consequence of having the singing behavior so sensitively tuned to hearing the pulses of other bats: the neural mechanism that motivates singing in a subset of males may itself not be variable enough to allow for differential expression of the behavior at sunset versus sunrise. It may also be the case that the social group benefits from having one or a few singing males remain in the roost throughout the night to facilitate their periodic returns for resting between foraging bouts. If a group of 50–100 bats contained 5–10 singers, and this subset of singing bats took turns going out to forage, the persistent singing at the roost might help returning bats save energy by facilitating more rapid localization of the roost. If singing serves this general function, however, then why do not both males and females show a similar propensity to sing, particularly considering that much of the year females roost almost exclusively with other females (McCracken 1984)?

In conclusion, the observations reported here lead us to hypothesize that singing may play a critical role in facilitating migration, especially during the spring. It may be that this behavior was reinforced by both natural and sexual selection by easing the burden of finding temporary roosts during migratory periods and also by enhancing the reproductive success of the singers. However, there is conflicting evidence regarding the role of the song as a territorial defense mechanism; singers often share roosts with many other non-singing, possibly subordinate, males, but there are also situations in which males aggressively defend their roosts from invading males. In this study we did not systematically count individuals or check the sexes of bats within the roost, as this was impractical. One possible explanation for the differences in territorial behavior associated with singing may be the presence or absence of females. If a singing male bat manages to attract a female to its roost it may become more protective of the female and under those circumstances be motivated to exclude other males. If on the other hand no females are present, the singing bat may be better off sharing the roost with other male conspecifics than roosting alone. These possibilities could be investigated experimentally in future studies.

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Chapter 10
Social Learning and Information Transfer in Bats: Conspecific Influence Regarding Roosts, Calls, and Food

Genevieve Spanjer Wright

Abstract Using social information can be an efficient way to respond to changing situations or learn skills. Most bat species (Order Chiroptera) are gregarious and could theoretically benefit from socially obtained information about food or roosts. Many bats experience opportunities for social learning, and recent years have seen a variety of studies addressing this phenomenon in the Chiroptera. Because bats are aerial, small, nocturnal, and emit calls outside the range of human hearing, they are notoriously difficult to study, and distinguishing between individuals when multiple bats are present can be especially challenging. Recent advances in technology, including high-quality synchronized video and audio recordings, and the use of passive integrated transponder (PIT) tags and radio-tracking, have allowed for detailed information to be obtained about individuals in multi-bat settings. Recent studies have shown that bats can learn from one another about food type, food location, and other food-related cues. In addition, social information can play a role in roost site selection and the acquisition and modification of vocalizations. Here, I review recent research documenting vocal learning in bats, as well as interactions between individuals in foraging and roosting contexts and the impact of these interactions on bats' behavior and success. I also report on novel findings wherein individuals of a frugivorous bat species display decreased foraging success in the presence of other naïve individuals and discuss possible reasons for this result. Finally, future directions for research on social learning in bats, which could employ such technologies as thermal imaging cameras, GPS tracking, and on-board microphones, are discussed.

10.1 Introduction

Relatively long-lived animals, particularly those whose food sources or roosts change seasonally and over the course of a lifetime, should benefit from the ability to learn new skills and gather new information throughout their lives. Flexibility,

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innovation, and learning abilities should be especially important for animals with these characteristics. Animals that are able to use social information (e.g., watching, listening, following, and imitating), in addition to individual learning, can respond more appropriately in unpredictable environments (Cavalli-Sforza and Feldman 1983; Boyd and Richerson 1985).

Group living animals, especially, may benefit from gaining information based on the behavior of others (Cavalli-Sforza and Feldman 1983; Boyd and Richerson 1985). This might include obtaining social information in a variety of ways, such as learning which food sources are safe to consume based on olfactory or taste cues from roostmates (e.g., Galef 1988), or learning a novel method of foraging or accessing food through interactions with, or observations of, a knowledgeable conspecific(s) (e.g., Lachlan et al. 1998; Rapaport and Ruiz-Miranda 2002; May and Reboreda 2005; Thornton and McAuliffe 2006). Obtaining social information in these scenarios might benefit the observer by preventing it from ingesting unpalatable items or increasing its foraging efficiency, respectively.

Bats, with their propensity for spending time in the company of conspecifics (and sometimes heterospecifics), relatively long lifespans, and challenges such as migrating, ephemeral roosts, and changing food sources, are ideal for addressing questions about social learning and information transfer. The term “social learning” has been defined in a variety of ways. It can be difficult to define and confine what behaviors can be categorized as social learning, and there can sometimes be overlap between social learning and other phenomena, such as communication. For the purposes of this chapter, I use this term in a broad sense, to encompass examples of information transfer and to describe any time an individual uses direct observation of or information from another animal gain a skill (e.g., how to handle prey, how to make a specific vocalization) or acquire information (e.g., where to find food, where to roost), i.e., “when individuals learn from information generated by the behavior of other individuals” (Giraldeau and Caraco 2000, p. 254).

While most bat species spend time in the company of conspecifics, there is a vast array of social structures represented in this group (Bradbury 1977; McCracken and Wilkinson 2000; Kerth 2008). Social organization can have an impact on several aspects of social learning. For example, if individuals roost or forage with kin or other stable groups wherein cooperation or reciprocity is likely, transferring information about food or roosts to individuals (or at least not behaving aggressively toward naïve individuals) should be favored (e.g., Kerth and Reckardt 2003; Ratcliffe and ter Hofstede 2005). Likewise, if stable groups use vocalizations for group recognition, social modification of calls (a form of vocal learning) is necessary for convergence of group members’ calls (e.g., Boughman 1998). In addition, if young bats stay with their mothers for a relatively long duration, learning foraging-related skills from one’s mother may be more important and practical (e.g., Wilkinson 1985). In contrast, bats without stable groups or that mostly forage alone should experience fewer opportunities for learning from others.

While social learning by bats has received relatively little study compared to some other aspects of bat social behavior, there has been an increase in this line of research in recent years. Wilkinson and Boughman (1999) summarize the research on foraging-related social influences on bats conducted prior to 2000; therefore this chapter will focus on foraging-related research that post-dates Wilkinson and Boughman (1999), and on non-foraging-related studies concerning social learning in bats. First, I will discuss roosting-related social learning and information transfer in bats, followed by the mounting evidence of vocal learning in various bat species. I will then outline more recent studies of social influences on foraging in bats, including previously unpublished data investigating the ability of *Artibeus jamaicensis* to learn socially about food location.

10.2 Roosting-Related Information Transfer

Species of the Order Chiroptera occupy a diverse range of roosts, including caves, mines, tree cavities, foliage, and the outside and interiors of buildings. While roost type varies, individuals of most species live in close proximity with conspecifics and sometimes with other species as well (e.g., Twente 1955; Swift and Racey 1983; Graham 1988). Questions regarding exactly how bats select specific roosts have not been fully answered, and the social aspect of this phenomenon is even more challenging to understand. However, there is evidence from multiple species that bats exchange information about roost location and suitability. For example, Wilkinson (1992) found that young evening bats (*Nycticeius humeralis*) follow experienced bats to a new roost site when excluded from their previous one, possibly by eavesdropping on the calls of the older bats.

Similarly, female Bechstein's bats (*Myotis bechsteinii*) exchange information about roost suitability (Kerth and Reckardt 2003). This fission-fusion species forms stable colonies of 15–40 individuals (Kerth et al. 2000), yet uses 50 or more day roosts during one reproductive season (Kerth and König 1999). These factors make information transfer related to roosts beneficial for maintaining group cohesion. Over the course of 2 years, the researchers presented maternity colonies with both suitable (accessible) and unsuitable (interior entranced blocked with mesh wire) roosts and recorded bat presence at each roost using passive integrated transponder (PIT-tag) readers. They found that significantly more bats were recruited to the suitable roost boxes. Naïve bats arriving at suitable roosts were significantly more likely to arrive within 3 min of an experienced bat compared with those arriving at unsuitable roosts, and recruited bats often arrived in groups with more than one experienced bat. The authors found no evidence of reciprocity or relatedness being factors in recruiting behavior, but postulated that the benefits of group living may drive the behavior. They did not think that bats at accessible roosts were using calls to recruit naïve bats, but they did not conduct audio recordings.

In contrast to the study described above, an experiment focusing on noctule bats (*Nyctalus noctula*) revealed that eavesdropping on conspecific echolocation calls emitted from cavity roosts was a crucial component for bats searching for cavities (Ruczynski et al. 2007). In this laboratory experiment, the researchers provided naïve bats with various social and nonsocial cues in a task requiring bats to find a cavity roost in a tree trunk. Bats found the roost opening significantly more quickly when playbacks of conspecific echolocation calls were emitted from the roost compared with searching with no extra cues. Subsequent research showed that bats of this species are also attracted to social calls being played back at potential roost sites (Furmankiewicz et al. 2011). For this experiment, which took place in the field with freely behaving bats, the authors recorded social calls from pregnant females in maternity roosts, and then played the calls back at artificial roosts. Bats responded by flying near or inspecting the roost from which social calls were emitted significantly more frequently than they inspected or approached roosts emitting background noise or no sound. Considering that this is a migratory species that changes roosts every few days and prefers roosts with fairly specific microclimate conditions (e.g., Ruczynski and Bogdanowicz 2005), individuals should benefit greatly by capitalizing on the roost discovery of others and may also benefit from keeping track of familiar individuals. Considering the high amplitude of the social calls and other factors, the authors (Furmankiewicz et al. 2011) suggest that bats might be using social calls from within the roost to help maintain group cohesion.

While cavity-roosting noctule bats respond to conspecific social calls from within roosts, a sophisticated system of using social calls to transfer information about roosts has been documented in another species. Spix's disk-winged bat (*Thyroptera tricolor*) roosts in furled *Heliconia* leaves and thus must change roosts as often as daily (Findley and Wilson 1974; Vonhof et al. 2004) yet maintains small cohesive groups for as long as almost 2 years (Chaverri 2010). Chaverri et al. (2010) discovered that to keep track of roosting locations (and the roostmates within), bats play a version of "Marco, Polo," with flying/searching bats emitting an "inquiry call," and the bat in the roost responding with a different call. A follow-up study revealed that flying bats (but not bats inside a roost) discriminate between the calls of group members and other bats, and respond preferentially to group members (Chaverri et al. 2012). These findings further support the idea that this call and response system promotes group cohesion as well as roost-finding. These studies highlight the intersection between roost selection and information transfer in bats. Learning about roost location and quality from others serves the dual purposes of finding a high-quality roost and ensuring that other bats will be present there, thus allowing individuals to continue to reap the benefits of group living, and in some cases, cohesion of a stable group.

10.3 Vocal Learning

Vocal learning can be defined as animals modifying existing vocalizations or acquiring new vocalizations based on conspecific influence. Though widely documented in birds, vocal learning is thought to be much less common in mammals, having been found in only a handful of mammalian groups (Janik and Slater 1997; Boughman and Moss 2003). Considering the strong reliance of many bat species on echolocation and the ever-mounting records of vocal communication from many species (e.g., Fenton 1985; Pfalzer and Kusch 2003; Chaverri et al. 2010; Knörnschild et al. 2010a; Carter et al. 2012; Wright et al. 2013), it is not surprising that at least some bat species utilize vocal learning. Researchers have found evidence of vocal learning for both echolocation and social calls, and it is important to remember that the two call types may not always be mutually exclusive. Echolocation pulses can convey information about attributes such as sex, age, familiarity, or individual identity (e.g., Masters et al. 1995; Kazial and Masters 2004; Voigt-Heucke et al. 2010; Jones and Siemers 2011), and bats may be able to extract information from the echoes returning from calls emitted primarily for a communicative purpose. Some evidence for vocal learning related to echolocation calls comes from horseshoe bats (*Rhinolophus ferrumequinum*). This species displays changes in its echolocation calls over the course of a lifetime, and Jones and Ransome (1993) discovered that pups' developing calls bore similarities to the calls of their mothers. In addition, there is evidence that Taiwanese leaf-nosed bats (*Hipposideros terasensis*), a CF-FM species, change the resting frequency of their calls based on the call frequency used by conspecifics, with call frequency convergence observed (Hiryu et al. 2006). While the two studies above provide evidence of a social aspect of echolocation call features, learning involved in the development or use of communicative calls has been observed in four bat species to date (see review by Knörnschild 2014; Prat et al. 2015). Newborn bats of many species emit isolation calls when separated from their mothers (e.g., Gould 1975; Thomson et al. 1985; Balcombe 1990), and in some species, such as lesser spear-nosed bats (*Phyllostomus discolor*), mothers reply with a directive call, thus aiding in mother–pup reunions. Esser and Schmidt (1989) found that in most of the pups they observed (6/8), the features of the isolation call converged on the acoustic features of their mothers' directive calls. However, this was an observational study, and genetic or maturation effects could not be ruled out. A follow-up, controlled study including one group of hand-reared bats that was acoustically isolated from conspecifics and a second group of bats that was exposed to playbacks of a maternal directive call supported these findings (Esser 1994). Specifically, pups exposed to auditory playbacks altered the call structure of their isolation calls to resemble that of the played back directive calls, while pups in the control group did not (Esser 1994).

Female greater spear-nosed bats (*P. hastatus*) roost in stable groups and use group-specific social calls to coordinate foraging (Wilkinson and Boughman 1998). Characteristics of these group-specific "screech calls" are the product of vocal learning. When young bats are switched between groups, both resident and new bats modify their social calls to converge on a new group-specific screech call (Boughman 1998). Similar to *P. hastatus*, the greater sac-winged bat (*Saccopteryx bilineata*) has been found to display learned group signatures (Knörnschild et al. 2012). This species displays resource-defense polygyny, with harem males attempting to retain their females (see Voigt et al. 2008) through various means. As *S. bilineata* pups mature, the isolation calls of pups within a group—regardless of relatedness—display a convergence of acoustic features, which is indicative of vocal learning (Knörnschild et al. 2012). This species also provides the first known example of a bat species displaying vocal imitation, wherein new vocalizations are acquired socially (compared with modifying innate vocalizations; Knörnschild et al. 2010b; Boughman and Moss 2003). Adult males use a complex song as a means of defending their territories (Behr and von Helversen 2004; Davidson and Wilkinson 2004), and pups of both sexes imitate the song emitted by their harem male (Knörnschild et al. 2010b).

Recent research on the Egyptian fruit bat (*Rousettus aegyptiacus*) shows a greater role of vocal learning than was previously understood in the development of this bat's vocal repertoire (Prat et al. 2015). While this species does not use laryngeal echolocation (it uses tongue clicks instead; Kulzer 1956), it emits a rich vocal repertoire. Prat et al. (2015) recorded vocalizations from young bats who either matured in a colony or were acoustically isolated from older bats (each pup in this group was alone with its mother, who remained silent with no other adults present) but were exposed to playbacks of conspecific calls. They found that pups raised with other bats developed the adult call repertoire. Isolated bats did not develop the full repertoire but mimicked the playbacks to which they were exposed. As vocal learning is demonstrated in an increasing number of bat species, questions arise about how prevalent the phenomenon might be amongst animals that rely so heavily on audition. With the evidence of vocal learning across a variety of bat species and involving both echolocation and communicative calls, this phenomenon may prove to be widespread within Chiroptera.

10.4 Social Learning of Food-Related Information

10.4.1 Overview and Previous Research

As discussed in the two previous sections, bats can learn vocal production and information about roosts from conspecifics. Unsurprisingly, evidence also continues to mount that bats can learn about food sources, types, and locations form one another, though still relatively few species have been tested for this capacity. Several studies have found that bats are attracted to the echolocation calls, particularly feeding buzzes, of foraging conspecifics, which can indicate the presence of food nearby (e.g., Barclay 1982; Balcombe and Fenton 1988; Fenton 2003; Gillam 2007). Gaudet and Fenton (1984) demonstrated that three species of captive insectivorous bats (*Myotis lucifugus*, *Epteiscus fuscus*, and *Antrozous pallidus*) learned a novel foraging task (taking food from an alligator clip) significantly faster via interaction with a knowledgeable conspecific compared with training by humans. In addition, a study of *Myotis myotis* and *M. oxygnathus* demonstrated cross-species social learning (Clarin et al. 2014). Bats in this study were trained to associate a light cue with a food reward, and naïve bats learned the task more quickly when allowed to interact directly with a knowledgeable bat than by merely observing a knowledgeable individual or without a knowledgeable bat present at all

(Clarin et al. 2014). Considering that many bat species regularly roost with and/or forage near heterospecifics, other cases of interspecific social learning seem likely.

Wilkinson (1987) showed that naïve lesser spear-nosed bats (*P. discolor*) found a single accessible food cup among sixteen faster when they were searching with a knowledgeable bat (versus searching alone). In addition, evening bats (*N. humeralis*) have been shown to exchange information by following conspecifics to foraging sites and roosts (Wilkinson 1992). For more details about research on social influences on foraging in bats conducted prior to 2000, please see Wilkinson and Boughman (1999). More recent years have seen an increase in experimental (versus observational) studies of social learning about food by bats. For example, Page and Ryan (2006) found that the frog-eating bat, *Trachops cirrhosus*, acquired a novel foraging behavior more quickly in the presence of a trained conspecific than alone or with another naïve bat. This experiment involved training bats to respond to an acoustic cue that signified food availability. A later study with the same species (Jones et al. 2013) found that bats' tendency to copy conspecifics depended on the success of individual foraging. Bats were presented with either reliable or unreliable feeding cues, and some individuals were paired with a trained tutor. Bats presented with unreliable cues and a knowledgeable tutor were significantly more likely to respond to the cue demonstrated by the tutor than bats presented with reliable cues or those without a tutor (Jones et al. 2013). These results indicate that bats are more likely to use information from others when individually-obtained information is not reliable.

One would expect that young animals are likely to benefit from social learning, and a lab study of big brown bats (*Eptesicus fuscus*) supports this idea. When young (<2 months old) and adult ($\geq$ 1 year old) naïve bats were paired either with bats who were experienced with a novel foraging task (taking a tethered insect while flying) or with other naïve bats, the bats who interacted with experienced individuals were significantly more likely to learn the foraging task (Wright et al. 2011). Furthermore, we found evidence that close following flight and attention to feeding buzzes was positively related to bats' social learning of the task (Wright et al. 2011).

As described above, young insectivorous bats may learn foraging skills from others (e.g., Wilkinson 1992; Wright et al. 2011), and vampire bat pups have been known to share feeding wounds with their mothers (Wilkinson 1985). While multiple studies demonstrate that bats learn about food from one another, evidence for actual teaching is more elusive. To qualify as teaching, the following criteria must be met: (1) the "teacher" must change its behavior in the presence of the naïve individual, (2) there is an initial cost to the teacher's behavior modification (e.g., loss of food), and (3) the naïve individual learns the behavior faster than it otherwise would have (Caro and Hauser 1992). Thus far, evidence of teaching in bats is scarce, but there is report of a single instance of teaching in pallid bats (*Antrozous pallidus*; Bunkley and Barber 2014). In this case, all three criteria of teaching were met when an adult female familiar with a laboratory feeding task approached and called to a naïve juvenile male before accessing the food source. This male subsequently learned the foraging task much more quickly than other naïve individuals.

While this observation could be indicative of more widespread behaviors, it is, of course, important to use caution when interpreting the results of a single observation. Controlled studies with a larger sample size could determine if this behavior is anomalous or common.

In addition to the interaction involving pallid bats, a study of free-living common big-eared bats (*Micronycteris microtus*) found that mothers provision their young with insect prey following weaning (Geipel et al. 2013). As the pups matured and became more successful in their own hunting attempts, provisioning, which was observed for 5 months, decreased in frequency. The authors propose that such provisioning introduces young bats to adult prey, allows them to learn acoustic images of the prey, and lets them practice prey-handling. Indeed, research with other mammals (e.g., meerkats; Thornton and McAuliffe 2006) has found that post-weaning provisioning serves to teach young animals how to handle (and perhaps recognize) prey (see Caro and Hauser 1992; Thornton and Raihani 2008). Young bats of various species have been shown to follow other bats to foraging and roosting sites (Wilkinson 1992), learn a foraging task via interaction with experienced bats (Wright et al. 2011), and potentially learn prey-handling skills through adult provisioning (Bunkley and Barber 2014; Geipel et al. 2013), yet the topic of how young bats learn to forage, hunt, and/or handle prey has scarcely been studied. Further research into this topic, especially conducted on free-living animals like the Geipel et al. (2013) study, would offer insight into how bats with diverse feeding habits become proficient at finding and consuming their food.

Most of the research described above involves animal-eating bats, but predatory species are not alone in being influenced by conspecifics in a foraging context. Short-tailed fruit bats (*Carollia perspicillata*) tested individually and in groups in a laboratory setting found food more quickly when flying with other bats (Wright 2012). This effect was seen regardless of whether any other bat present was knowledgeable of the food's location in advance, and the results indicate that social facilitation (enhanced feeding behavior influenced by mere presence of conspecifics) was at play (Wright 2012). Bats were presented with multiple mesh feeders, only one of which contained accessible banana. Five individuals tested alone and in a group found the food more quickly in a group. While the presence of a knowledgeable bat had no measureable effect on bats' performance (and the bat that knew of the food's location was not always first to feed), the results showed that the same few individuals fed first more often than expected by chance (Wright 2012). Considering that someone must be the "leader" if animals are following one another to a food source, it is possible that some individuals are more prone to being the putative leader by often finding food first. Additional research could help rule out other possible explanations for the same bats often feeding first.

While animals often learn about food from conspecifics during foraging, information exchanged in the roost can also be beneficial. Ratcliffe and ter Hofstede (2005) demonstrated that captive *C. perspicillata* are more likely to eat a novel flavor of food if they have been exposed to a bat that has recently consumed this food. Presumably, bats smelled and tasted the food flavor on their roostmates' fur or breath. Likewise, tent-making bats (*Uroderma bilobatum*) preferred food their roostmates had recently consumed (O'Mara et al. 2014) in both a captive and natural roost setting. This study also went a step further and found that bats preferred food their roostmates had actually consumed over food whose odor was present on the fur but had not been eaten. This indicates that bats selectivity use odor cues from conspecifics' breath (O'Mara 2014).

10.4.2 (Mis) Information Transfer in Jamaican Fruit-Eating Bats

When deciding whether to rely on social versus individual information, animals should consider the reliability of the available information. If individually-obtained information (e.g., trial-and-error, searching alone) is unreliable, individuals should use socially-obtained information (e.g., Jones et al. 2013). While social learning can be and often is beneficial to naïve individuals, basing one's behavior on the actions of others can instead have negative impacts if, for example, the "demonstrator" is not knowledgeable or reliable. In such situations, which could also include a rapidly changing environment, relying on social information could result in suboptimal or maladaptive behavior (Giraldeau et al. 2002; reviewed by Rieucau and Giraldeau 2011). Research experimentally showing that animals socially acquire suboptimal behavior is scarce, and in some cases, the risk of being alone versus in a group must be weighed against the advantages of an otherwise preferred behavior (Rieucau and Giraldeau 2011). My research with Jamaican fruit-eating bats (*Artibeus jamaicensis*) provides an example of individuals tending toward suboptimal behavior, apparently based on the behavior of conspecifics.

In March–May 2008, I conducted a study examining the effects of conspecifics on foraging behavior and success in *A. jamaicensis*. This species roosts in harems and can be found foraging in large numbers at fruiting fig trees, but there is mixed evidence regarding whether this bat forages in cohesive groups (see Ortega and Castro-Arellano 2001), and it is not known if *A. jamaicensis* exchange information about food. I wanted to find out if these bats were helped or hindered by the presence of others in a foraging setting, and what related mechanisms might be at play. To address these questions, I captured (in mist-nets) and tested 31 adult, non-lactating *A. jamaicensis* on Barro Colorado Island in Panama.

Bats were presented with three food-finding tasks of increasing complexity (Fig. 10.1) either in groups of four or five bats ($n = 19$) or individually ($n = 12$). Bats were tested nightly in a screen tent (3.4 × 4 m with 2.4 m center height) after at least 9 h of food deprivation. Individuals were marked wtih reflective tape cut into individually-distinct shapes and temporarily affixed to their backs.

The food-finding task was as follows: In level 1, in one corner of the tent, a mesh partition with a single opening large enough for bats to fly through ($\sim$50 cm diameter) led to a single food cup containing banana. In level 2, the feeding area was divided into two parts, one with an accessible food, and a second cup containing banana but covered in mesh such that bats could smell but not consume it. In level 3, the feeding area was divided into four parts, with three sections

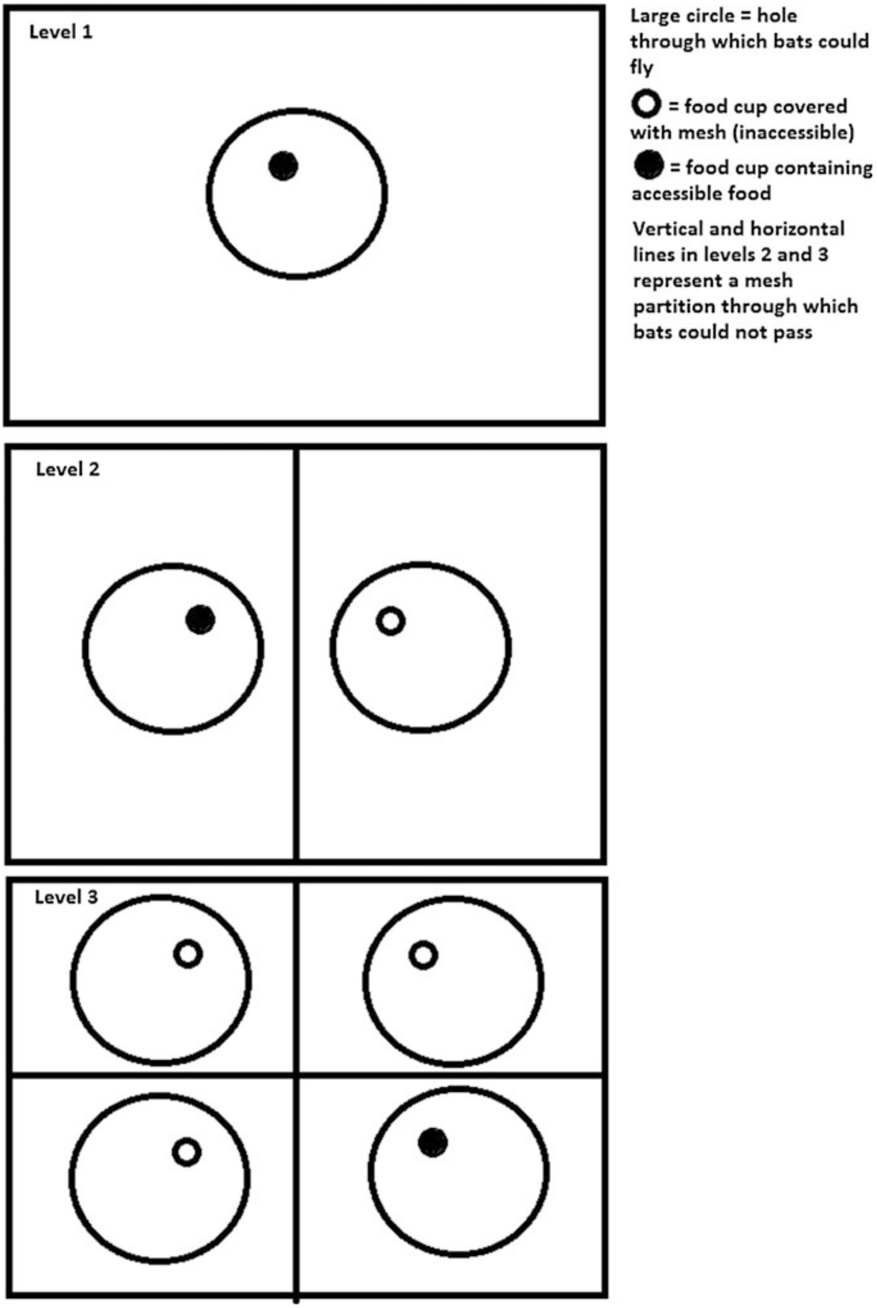

Fig. 10.1 Schematic of experimental setup for *A. jamaicensis* foraging study. Bats were tested individually or in groups. The location of the accessible food (banana) was not always the same. Bats only showed a difference in performance based on conspecific presence for the most complex task (level 3). Bats flying in level 3 took longer to access the food when flying in groups versus alone

containing inaccessible food and one containing the accessible food cup (Fig. 10.1). In levels 2 and 3, bats could not move from one compartment to another without first exiting the hole through which they had entered (Fig. 10.1).

Each bat or group of bats was presented with all three levels (one level per night, with two exceptions when bats were given the same level for a second night). No individual was trained or given any information regarding the accessible food's location prior to testing. I tested bats for 4 h, or until every bat had accessed the food, with a break after 2 h of testing. The location of the accessible food was not the same for each group/individual. Based on real-time observations and subsequent analyses of video recordings, I assessed the time taken for each bat to feed, time spent at the food source, time spent at inaccessible (closed) food, attempts to access the inaccessible food, and interbat interactions. Due to the non-normal distribution of the time data, data were categorized as follows (multinomial distribution): bat accessed food within 30 min; between 31 and 120 min; or did not feed within 120 min (this includes bats that did not access the food at all). A generalized linear mixed model was used (GLMM), and levels 1, 2, and 3 were analyzed separately.

For each of the three levels, the trend was toward lone bats accessing the food more quickly than those flying with conspecifics. For levels 1 and 2, there was no significant difference in time to access the food between individual/lone bats (control; $n = 12$) and bats flying in groups ($n = 19$ for level 1 and 18 for level 2; $P > 0.05$ for both). However, in the most complex task (level 3), bats tested alone ($n = 12$) accessed the food significantly faster (mean ± SD = 66 ± 86 min) than bats tested in groups ($n = 19$; mean ± SD = 150 ± 96 min; $F_{1.28} = 6.07$; $P = 0.02$; Fig. 10.2).

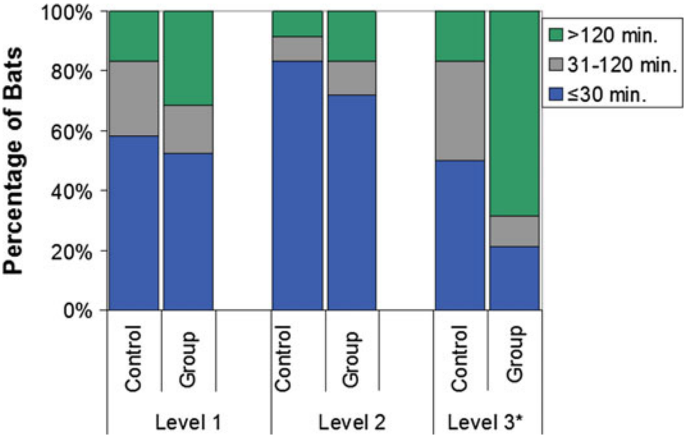

Fig. 10.2 Time for *Artibeus jamaicensis* to access food flying alone (control; $n = 12$) versus in groups ($n = 19$ for levels 1 and 3; $n = 18$ for level 2) in food-finding tasks with three levels of complexity (level 1 = simplest; level 3 = most complex). * = a significant difference between control and group

These findings show that social context had a significant impact on bats' foraging behavior. Bats' foraging speed was unaffected by the presence of conspecifics when the task was relatively simple, but bats fared better alone when the foraging task was complex. To understand why presence of conspecifics had a negative impact on bats' food-finding speed in level 3, I drew additional information from the video recordings and tested measures allowing me to address two hypotheses. If bats were taking longer to access the food because they wished to avoid leading other bats to the food source or because they feared aggression from other bats, I expected bats to leave the foraging area quickly when other individuals are present. In contrast, if bats in groups take longer to access the food because they are confused or distracted by conspecifics' search behavior, I expected bats to spend more time at the inaccessible food when conspecifics are nearby (and/or to visit the inaccessible food more frequently than lone bats).

To quantitatively address these hypotheses, I calculated how often bats flying in groups or alone visited closed feeding cups (inaccessible food), how long bats spent at the accessible food source, and how long bats spent at closed feeding cups overall and when another bat was nearby (multinomial distribution; GLMM). There was a high level of individual variation regarding time spent at the accessible food, and there was no consistent trend or significant difference in time spent at the food source for bats flying in groups versus alone at any of the three levels. Likewise, there was no significant difference in the frequency with which lone vs. group bats visit closed feeding cups, nor the overall time bats in groups versus alone spend at closed feeding cups. However, the data show that bats flying in groups spent significantly more time at closed feeding cups if another bat is in the same section of the "maze" ($n = 17$) compared with time spent at closed cups with no other bat in the same section ($n = 59$; $F_{1.70} = 8.57$; $P < 0.01$). On average, bats spent five times longer near/trying to access closed feeding cups when another bat was nearby (25 s vs. 125 s.; Fig. 10.3). This finding supports the hypothesis that individuals are confused or distracted by one another's search behavior.

In a roundabout way, the results of this experiment support the idea of social learning in *A. jamaicensis*, since bats spent more time trying to consume inaccessible food when another bat was nearby. Bats appeared to look to conspecific behavior for

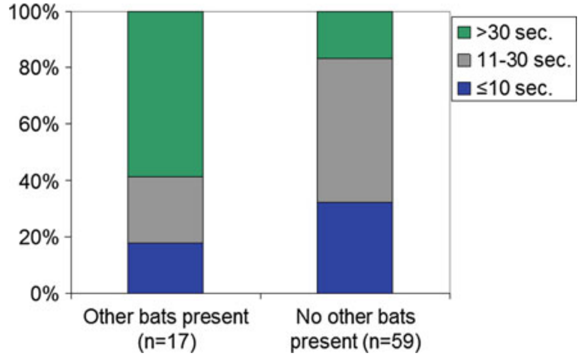

Fig. 10.3 Time spent by Jamaican fruit-eating bats flying in groups trying to access inaccessible food. When another bat was nearby, bats spent, on average, five times longer near the inaccessible food source. The difference was statistically significant ($F_{1.70} = 8.57$; $P > 0.01$)

clues about where and how to access food. However, given the nature of the task and that all bats were initially naïve, bats were slower, not faster, to find the accessible food source when flying with others, but only in the most complex task (level 3). In the simpler tasks (levels 1 and 2), there was no difference in food-finding speed between bats flying alone and those flying in groups, perhaps indicating less of a need for social information when the task is relatively straightforward. It was only when the chances of finding inaccessible food outweighed those of finding accessible food three to one that social context became relevant.

These findings highlight the importance of a reliable demonstrator for animals relying on social information. Because none of the bats in this experiment were trained or had prior experience with the accessible food's location, there were no knowledgeable "leaders," and individuals' decision to rely on social information was more likely to lead them to closed food cups versus the single cup with accessible food. The idea that naïve "bystanders" can actually hinder foraging success ("tutor dilution"; Giraldeau and Caraco 2000) has also been found in experiments involving flock-foraging birds (e.g., Lefebvre and Giraldeau 1994). In addition, experiments with guppies found that fish will choose a longer route to food when exposed to demonstrators exhibiting this behavior (Laland and Williams 1998), but choose the shorter route when swimming alone (Bates and Chappell 2002). This difference indicates that the benefits of staying with the group must be weighed against otherwise optimal or efficient behavior (e.g., a shorter route). My experiment did not allow me to distinguish between bats believing that conspecifics could lead them to food versus choosing to forage near other individuals for other reasons (e.g., anti-predatory measures). In situations like those described above, the tendency of individuals to choose social information over individual information becomes a hindrance rather than a benefit.

In addition to being confused or distracted by the behavior of unknowledgeable conspecifics, other factors that either played a more minor role and/or were difficult or impossible to quantify may have had an impact on the bats' behavior. Such factors, evidence of which were observed in real time and/or in video recordings, include kleptoparasitism (food-stealing) or aggression, scrounging (consuming food other bats dropped), following behavior, and pre-existing inter-individual relationships. Bats were occasionally observed squabbling audibly or taking food from one another. When one bat landed at the food source, the resident bat sometimes fled but often stayed, and bats sometimes landed at the food source in quick succession. I occasionally saw bats eat food that others had dropped. Because bats were wild-caught in the forest just before testing, I had no information about bats' relatedness, familiarity with each other, or any dominance hierarchies among individuals. Additionally, bats are unlikely to encounter a situation in the wild wherein they can smell food but not access it. In summary, this experiment revealed that complexity/difficulty of a task affects whether animals rely on social information, as well as the importance of a reliable demonstrator/leader if social learning is to be beneficial.

10.5 Conclusions and Future Directions of Research

As described in this chapter, a variety of bat species have shown the capacity for learning from others in a variety of contexts (Table 10.1), yet the vast majority of bat species have not been tested for this phenomenon. Because of bats' small size, nocturnal lifestyle, rapid movements, aerial nature, and propensity for roosting and flying in groups that can number hundreds or thousands of individuals, behavior of individuals is notoriously difficult to study in a natural environment. Traditionally, research involving social learning has included two individuals at a time—one knowledgeable about a given task and one naïve—in a controlled laboratory setting. While important information can be gained from this set up, recent advances in technology have allowed for more experiments involving more than two individuals in more naturalistic settings.

In a captive setting, synchronized high-speed video cameras and microphones offer detailed re-creation of bat flight paths and interactions coupled with their vocalizations. This allows researchers to study exactly how bats are interacting with one another, both physically and acoustically, as they engage in foraging or other behaviors. As advances in technology continue to shrink the size of electronic components, on-board microphones for bats are being developed and have already been used for studies focusing on echolocation (Hiryu et al. 2008; Boonman et al. 2013). Such microphones allow for detailed information about the echolocation (Cvikel et al. 2014) and social calls emitted by multiple individuals flying together and can give researchers insight into what each bat says and hears as it interacts with conspecifics.

Additionally, the use of PIT-tags lets researchers know which bat passes through a certain point at a certain time, as well as allowing for detailed records of the behavior of many individuals freely behaving together. Studying free-living bats in the wild offers special challenges, but technologies such as thermal cameras and PIT-tags are useful tools. Radio-tracking has long been used to track the location of individual bats from roost to foraging site and back, and more recent efforts using GPS trackers affixed to bats (Tsoar et al. 2011; Cvikel and Yovel 2014; Cvikel et al. 2015) further enhance the available data. As the devices described above continue to be improved upon and perhaps shrunk even more, opportunities for studying social learning and information transfer among free-living bats in roosts and at foraging sites should expand.

While evidence for vocal learning exists for only a handful of Chiropteran representatives thus far (see above), this phenomenon has been tested in only a tiny fraction of bat species, and there is a growing number of studies showing group-specific signature calls in bats (e.g., *P. hastatus*—Boughman 1998; *S. bilineata*—Knörnschild et al. 2012; *T. tricolor*—Gillam and Chaverri 2012). This, combined with the fact that social vocalizations have been reported for a wide variety of species (e.g., see Fenton 1985; Pfalzer and Kusch 2003), provides fertile ground for additional experiments investigating vocal learning in bats. As a taxonomic group with over 1200 representatives, many of whom rely heavily on

Table 10.1 Social learning and information transfer in bats

Species	Type of social learning observed	Key findings	Publication(s)
Eptesicus fuscus	FR	Learned to obtain food in new ways by observing and/or interacting with knowledgeable conspecifics	Gaudet and Fenton (1984), Wright et al. (2011)
Antrozous pallidus	FR	Learned to obtain food in new ways by observing conspecifics; teaching food-handling skills	Gaudet and Fenton (1984), Bunkley and Barber (2014)
Carollia perspicillata	FR	Acquired flavor preference based on what roostmate had eaten; faster food discovery with conspecifics present	Ratcliffe and ter Hofstede (2005), Wright (2012)
Artibeus jamaicensis	FR	Spends more time at inaccessible food when conspecifics are present	This chapter
Phyllostomus hastatus	VL	Bats within a group alter calls to converge with one another	Boughman (1998)
Trachops cirrhosus	FR	Bats learn socially to respond to an acoustic cue indicating food; bats are more likely to use social information when individual information is unreliable	Page and Ryan (2006), Jones et al. (2013)
Saccopteryx bilineata	VL	Learned group signatures; pups of both sexes imitate male song	Knörnschild et al. (2010b), (2012)
Rousettus aegyptiacus	VL	Pups develop adult repertoire only if exposed to calling adults; acoustically isolated pups develop elements of calls played back to them	Prat et al. (2015)
Thyroptera tricolor	RR	Bats call to one another in a “Marco, Polo” fashion to find/broadcast roost location	Chaverri et al. (2010), Chaverri and Gillam (2016)
Hipposideros terasensis	VL	Change resting frequency of calls to converge with that of roostmates	Hiryu et al. (2006)
Nycticeius humeralis	FR, RR	Inexperienced bats follow others to foraging sites and roosts	Wilkinson (1992)
Myotis bechsteinii	RR	Bats recruit conspecifics to suitable roost boxes	Kerth and Reckardt (2003)
Myotis myotis	FR	Bats socially learned to respond to a light cue indicating food; inter-species social learning observed with *M. oxygnathus*	Clarin et al. (2014)
Myotis oxygnathus	FR	Bats socially learned to respond to a light cue indicating food;	Clarin et al. (2014)

(continued)

Table 10.1 (continued)

Species	Type of social learning observed	Key findings	Publication(s)
		inter-species social learning observed with *M. myotis*	
Micronycteris microtus	FR	Mothers provision insect prey to pups, which may help pups learn acoustic images and handling techniques for prey	Geipel et al. (2013)
Myotis lucifugus	FR	Learned to obtain food in new ways by observing conspecifics	Gaudet and Fenton (1984)
Nyctalus noctula	RR	Bats respond to echolocation and social calls from cavities to find roosts	Ruczynski et al. (2007), Furmankiewicz et al. (2011)
Phyllostomus discolor	VL	As pups grew, their isolation calls shared features with their mothers' directive calls	Esser and Schmidt (1989), Esser (1994)
Rhinolophus ferrumequinum	VL	Pups' echolocation call features are influenced by maternal call features	Jones and Ransome (1993)
Uroderma bilobatum	FR	Bats prefer food recently consumed by a roostmate and prefer food on a roostmate's breath to that on its fur alone	O'Mara et al. (2014)

FR Food or foraging-related
RR Roost-related
VL Vocal learning

acoustic information for orientation and/or communication, vocal learning is likely much more common among Chiroptera than is currently known. A final direction of research with relatively few representative studies is the intersection of social learning and vocal communication. As discussed previously, it is known that some bat species modify or acquire vocalizations based on the calls of conspecifics. In addition, social calls can inform other bats of roosting locations, including helping them to find new roosts.

While the inherent intent of vocal communication is to convey information to other individuals, little is known about the importance of social calls for bats learning about food from others. *Phyllostomus hastatus* use social calls to coordinate foraging (Wilkinson and Boughman 1998), but this is arguably as much about group cohesion as foraging itself. Social calls have been recorded from other species during foraging (e.g., *Pipistrellus pipstrellus*—Barlow and Jones 1997; *E. fuscus*—Wright et al. 2013, 2014), but none of these calls are known to facilitate learning prey location or handling by other bats. Additionally, there have been anecdotes of bats emitting apparent social calls in a social learning context (e.g., during potential teaching in *A. pallidus*—Bunkley and Barber 2014). During the time that young bats are learning foraging or prey-handling skills, or when stable groups of bats are foraging together, it seems reasonable that social calls might be used to convey information about resource location or prey capture/handling skills. Future studies focusing on the potential value of communicative calls for social learning may yield fascinating results.

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Part III
Ecological Aspects of Roosting and Foraging Social Behavior

Chapter 11
Indiana Bat (*Myotis sodalis*) Day Roost Selection in the Southeastern Ontario Lake Plain of New York State

Michael S. Fishman

Abstract Available habitat for the endangered Indiana bat (*Myotis sodalis*) varies widely across the species' broad range and the species' degree of habitat use specificity is not known; therefore, it is necessary to characterize the species' habitat use patterns regionally to provide suitable guidelines for wildlife managers to conserve the species throughout its range. Understanding day roost characteristics is particularly important because habitat suitability for Indiana bats is thought to be based on the availability of suitable day roost structures. Despite having been extensively studied at the core of their range, few studies of Indiana bat day roost characteristics have been published from the northeast periphery of the species' range, and no studies have been published from central New York State, where populations have been in steep decline due to White-Nose Syndrome since 2006. I studied day roosts of 20 female and 7 male Indiana bats in the Ontario Lake Plain northwest of Syracuse, New York, USA during the spring of 2006 and summers of 2007 and 2008 and identified 96 individual Indiana bat roost trees. Indiana bats roosted in 10 species of trees, of which *Carya ovata*, *Acer* spp., and *Ulmus americana* were most frequent. The mean diameter of roost trees was 41.55 ± 7.53 cm, which was similar to roost trees in other regions, but larger than the mean diameter of available trees in the same stands used by roosting Indiana bats. Male and female bats used similarly sized trees. I conclude that size of roost trees in central New York are similar to those throughout the Indiana bat's range, that the most frequently selected tree species differ regionally, and that patterns of male versus female roost selection varies regionally. This study provides regionally specific quantitative and qualitative metrics by which managers can identify potential Indiana bat habitat for land use planning and conservation.

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11.1 Introduction

The 2013 Indiana bat (*Myotis sodalis*) summer survey guidelines (USFWS 2013) required for the first time a documented habitat assessment as their first step to determine prospective survey locations. The Draft Recovery Plan for this federally listed endangered species (USFWS 2007) identified as one of its criteria for recovery: “conserve and manage summer habitat to maximize survival and fecundity.” A climate change habitat predictive model for Indiana bats suggested that habitat management for this species’ maternity colonies in the northeastern United States was, “critical as these areas will most likely serve as climatic refugia” (Loeb and Winters 2012). Identification and conservation of summer habitat for Indiana bats requires an accurate and consistent definition of such habitat, which has been elusive because of the variety of habitats used by this species across its range (Kurta et al. 2002). Whereas wildlife selects habitat hierarchically across multiple spatial scales (Johnson 1980), bat distribution, diversity, and population size is considered disproportionately dependent on the availability of suitable roost structures—a strictly local scale phenomenon (Humphrey 1975; Perkins 1996; Jung et al. 1999). Moreover, Indiana bats migrate to the same maternity areas year after year (Kurta and Murray 2002), and exhibit interannual fidelity to summer roost tree networks, which exhibit little variation from year to year (Silvis et al. 2014). Therefore, identification of suitable habitat for Indiana bats depends strongly on accurate identification of suitable roost structures for this species. Although Indiana bat roost structure features have been widely studied across the species’ range (Kurta et al. 1993; Callahan et al. 1997; Foster and Kurta 1999; Ford et al. 2002; Kurta 2002; Ritzi et al. 2005; Britzke et al. 2006; Watrous et al. 2006), roost trees and structures have been found to be highly variable, necessitating regional characterization of roost structure metrics to accurately identify suitable potential roosts. Two of the previously conducted studies of Indiana bat roosts were conducted in the northeastern extent of the species’ range (Britzke et al. 2006; Watrous et al. 2006). Both studies were conducted in the Champlain Valley of New York and Vermont, and only Britzke et al. (2006) studied roosts used during spring emergence and dispersal. Further study of Indiana bat roosts in the northeastern United States is warranted to determine whether possible differences exist in roost metrics by region.

Defining regional roost characteristics for the Indiana bat in central New York will provide a useful, region-specific tool for wildlife managers to accurately identify potentially appropriate roost structures for this endangered species in this region. New York is important because prior to population declines from White-nose Syndrome, a fungal infection that has decimated bat populations throughout the Northeast (Frick et al. 2010), New York’s Indiana bat population represented 11.3 % of the total range-wide population in 2007 (USFWS 2007), and had been rapidly growing at an average annual rate of 15.5 % for more than 4 years (King 2012). Loeb and Winters (2012) recently predicted that habitat management for Indiana bat maternity colonies in the northeastern extent of their range is critical as these areas will likely serve as climatic refugia for the species within the next 50 years under predicted climate change models. Identifying suitable potential roost structures in this region will enable wildlife managers to identify potential habitat areas to target for conservation. To this end, I characterized the day roosts of 27 Indiana bats in the Ontario Lake Plain of central New York State by size class, species, condition (live or dead), and solar exposure and compared my results to available trees within the same forest patches to determine: (1) whether Indiana bats selected roost trees in proportion to their availability, or whether they showed preference for trees with certain characteristics and (2) whether male and female Indiana bats selected similar roost trees.

11.2 Methods

11.2.1 Study Area

The 2006 study area included a known Indiana bat hibernaculum in the Town of DeWitt, Onondaga County, New York and spring and summer day roost locations in the Ontario Lake Plain east, north, and west of the City of Syracuse, in Onondaga, Oswego, and Cayuga Counties, New York (Fig. 2.1). The study area falls within the Ontario Lowlands Ecoregion, whereas the Champlain Valley area studied by Britzke et al. (2006) and Watrous et al. (2006) fell within the Champlain Lowlands Ecoregion (Bryce et al. 2010). While these lowlands share some common traits, such as limestone soils and climates tempered by large bodies of water, they differ in annual rainfall. The Champlain Valley falls within the rain shadow of the Adirondack Mountains (Northeast Highlands Ecoregion), and is therefore drier than the Ontario Lowlands. The Ontario Lowlands fall within the lake effect precipitation zone of Lake Ontario, receiving higher rainfall than the Champlain Valley because of the orographic effect of the Finger Lakes Highlands to the south, and the Tug Hill Plateau to the east (Bryce et al. 2010).

Two of the roost locations identified in spring 2006 were subsequently used as bat capture sites. During the summer of 2006, bats were captured at sites in a forested floodplain of Sixmile Creek, about 1.5 miles north of Peter Scott Swamp, in the Town of Schroeppel, Oswego County, New York. During the summers of 2007 and 2008, capture sites were situated in a forested floodplain area of the Seneca River in the Town of Salina, Onondaga County, New York.

11.2.2 Capture, Radio-Marking and Tracking

Adult reproductive female Indiana bats were manually captured from a hibernaculum cave in DeWitt, NY in cooperation with the U.S. Fish and Wildlife Service

Fig. 2.1 Study area in the southeastern Ontario Lake Plain of Oswego, Onondaga, and Cayuga Counties, New York, USA where Indiana bat (*Myotis sodalis*) day roost characteristics were evaluated

New York Field Office and New York State Department of Environmental Conservation, on 20 April 2006 as part of a spring emergence and dispersal study coordinated by those agencies. Captured bats were fitted with Holohil Model LB2 radio transmitters (Holohil Systems, Ltd., Carp, Ontario, Canada), released at the hibernaculum site, and subsequently tracked to spring roosts as they dispersed from the hibernaculum to their summer roosts.

Four-tiered nylon mist nets were used to capture Indiana bats from Indiana bat day roost areas from June to July 2006, and June to mid-August 2007 and 2008. Mist nets were 38 mm mesh, 50/2 nylon nets, ranging from 2.6 to 12 m wide, and measuring 2.6 m high (Avinet, Inc., Dryden, New York), set across watercourses and paths through wooded areas, and were used as single net sets or stacked up to 3 nets high to reach the tree canopy near previously identified Indiana bat roost trees (Kunz and Kurta 1988; USFWS 2007). Holohil Model LB2 radio transmitters weighing 0.3–0.35 g were attached to the interscapular area of the dorsum of each bat that weighed more than 6.5 g, using Skin-Bond surgical cement (Smith & Nephew, PLC, London, UK) as an adhesive (Brigham 2006). Radio transmitters each had unique frequencies and pulse rates to enable identification of individual bats by radio signal.

Bats were radio-tracked daily for 1–17d, depending on the battery life or attachment duration of each transmitter, using Communication Specialists' model R-1000 receivers and model RA-XXX 3-element Yagi antennas (Communication Specialists, Orange, CA, USA) to locate day roosts. Captured bats were assumed to be typical representatives of the larger population from which they were drawn, and to act independently, and there is no data to conclude otherwise. Day roosts were identified to specific tree by tracking bats to each roost and confirming the particular roost tree by detecting the marked bat emerging from it at dusk. Location coordinates of day roosts were determined with hand-held 12-channel global positioning system (GPS) units accurate to ±30 m.

11.2.3 Roost Tree Characterization

Roost trees were identified to species, and roost tree diameter at breast height (DBH) was measured for all roosts in all years. The total height of each roost tree and the height of each roost location within each roost tree were estimated visually during the 2006 field season and measured with a Brunton Clino Master clinometer (Brunton Outdoor Group, Riverton, WY, USA) during the 2007 and 2008 field seasons. Additional roost tree co-variates were measured for each roost tree as suggested by previous studies (Menzel et al. 2001; Kurta et al. 2002; Kurta 2004; USFWS 2007): tree condition, expressed as alive (containing living leaves) or dead (containing no leaves), and solar exposure, expressed as canopy cover immediately around the roost tree (*Closed*—roost tree crown completely overlapped by adjacent tree crowns; *Open*—tree canopy above the roost tree sufficiently open to allow direct sunlight exposure onto the bole of the tree for at least a portion of the day).

Available roost tree resources were determined with an inventory of available trees in two woodlots, each known to contain multiple occupied roost trees. Starting at a random point in each woodlot, 100 trees >10 cm DBH were identified in a 100 m square grid with parallel transects set every 10 m, and sampling stations set every 10 m along each transect. The tree of >10 cm DBH nearest to each sampling station was identified to species, DBH was measured, and it was assessed for condition and canopy closure, using the same criteria that were used for roost trees. Minimum tree size was set at 10 cm DBH because smaller trees were used by Indiana bats very infrequently and are generally not sufficient to provide suitable roosts for maternity colonies.

11.2.4 Data Analysis

I tested the null hypothesis that bats selected trees for roosting in proportion to their availability, contrasting mean DBH of all roost trees to that of mean DBH of trees available within the forest stands used by bats for roosting. Mean DBH of male and female roost trees were also compared to test the null hypothesis that male and female roost tree DBH was equal. Contrasts were made with a two-tailed *t*-test with a confidence level of $\alpha = 0.05$ (Bluman 2006). Size class distributions of roost tree species, live and dead trees, and trees used by males and females were compared with available tree species using *G*-tests (McDonald 2009) to test the following null hypotheses: Indiana bats (1) used size classes of each roost tree species in proportion to their availability; (2) used live and dead trees in proportion to their availability; and (3) males and females both used tree species in similar proportions relative to their availability. Classes with fewer than 5 individuals were combined or omitted for these analyses to avoid marked deviation of calculated *G* statistics from tabulated *G* statistics for each *G*-test (McDonald 2009).

11.3 Results

Ten reproductive female Indiana bats were tracked from their capture place at the main hibernaculum to their summer roosting areas. One female was captured near a roost site and was tracked to multiple roosts in 2006. Five female Indiana bats were captured and radio-tracked in 2007, and 12 Indiana bats (5 females and 7 males) were captured and radio-tracked in 2008. Bats were radio-tracked for 6.88 ± 0.79 d (range: 1–17 d). Tracking these bats enabled identification of 172 day roosts in 96 individual trees.

The mean number of roost days per tree was 1.58 ± 0.14 d, and the maximum period any one tree was occupied by an individual bat was 12 d. Bats roosted in dead and live trees, although proportions of each varied by species of tree (Fig. 2.2). In relation to tree condition, *Acer* species snags were selected for roost

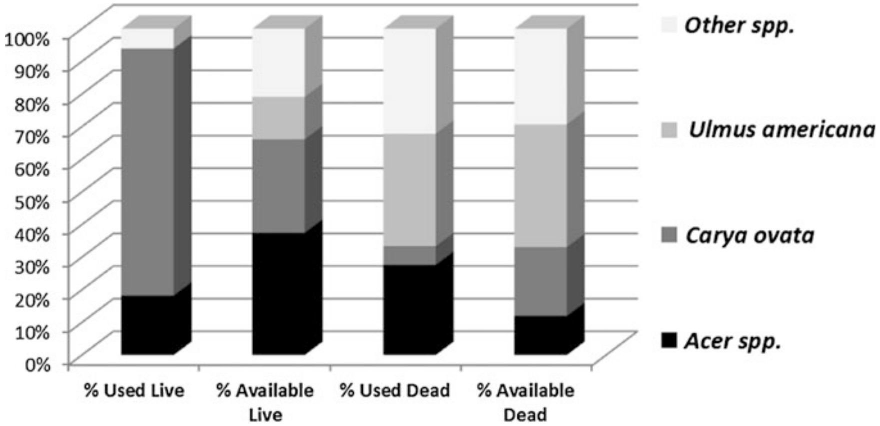

Fig. 2.2 Comparison of live and dead species of Indiana bat roost trees with available trees in central New York State, 2006–2008

Table 2.1 Number, frequency of use, condition, and roost type of each roost tree species used by Indiana bats (*Myotis sodalis*) in Central New York, 2006–2008

Scientific name	Common name	# of roosts	# of days	# Live/dead (%)	# Bark/crevice (%)
*Acer spp.**	Maple species	31	74	6/24 (20/80)	21/4 (84/16)
Carya ovata	Shagbark hickory	19	29	15/3 (83/17)	15/0 (100/0)
Fraxinus pensylvanicum	Green ash	1	1	0/1 (0/100)	1/0 (100/0)
Liriodendron tulipifera	Tulip poplar	1	5	0/0 (0/0)	0/1 (0/100)
Quercus alba	White oak	1	2	0/1 (0/100)	1/0 (100/0)
Quercus bicolor	Swamp white oak	3	6	0/3 (0/100)	2/0 (100/0)
Salix nigra	Black willow	2	10	0/2 (0/100)	2/0 (100/0)
Ulmus americana	American elm	10	15	0/10 (0/100)	9/0 (100/0)
Unknown sp.	Unidentified species	28	30	1/6 (14/86)	5/1 (83/17)
Total		96	172	22/50 (31/69)	56/6 (90/10)

*includes: *Acer rubrum*, *A. saccharinum*, *A. saccharum*, and maples not identified to species

trees significantly more frequently (80 % vs. 20 %) than live *Acer* species, while only 23 % of available *Acer* species trees were snags. All (100 %) *Ulmus americana* roost trees were snags, but only 73 % of available *Ulmus americana* were snags. Conversely, live *Carya ovata* were selected for roost trees far more frequently (83 %) than were snags of that species (27 %) (G-test: $G_{\text{adj}} = 14.7$, df = 3, $P = 0.002$). This indicates a significantly greater probability of *Acer* species and *Ulmus americana* selection as snags rather than live trees, and of *Carya ovata* selection as a live tree, rather than as a snag.

Most observed roosts were under loose bark ($n = 156$), but a few roosts ($n = 6$) were located in crevices created by cracked or broken tree limbs. Ten of the roosts could not be clearly identified as bark or crevice. Bark roosts occurred at least once in all tree species except *Liriodendron tulipifera*. Of the crevice roosts, four were in *Acer* species, and *Liriodendron tulipifera* and unkown species had one each (Table 2.1).

Mean DBH of all roost trees used by Indiana bats was 41.6 ± 7.5 cm and the mean height was 18.3 ± 1.4 m ($n = 96$). Mean height of all roost locations within all roost trees was 10.11 ± 1.46 m (range: 3–18, $n = 16$), and the proportion of roost location height/roost tree height was 0.53 ± 0.06 (range = 0.24 to 0.92, $n = 16$).

Mean DBH and height of male and female roost trees were found to be similar in this study area (DBH, $t = -1.26$, df = 26, $P = 0.22$; height, $\alpha = 0.05$: $t = -0.999$, df = 17, $P = 0.33$), but there was smaller variance in male roost tree size ($\sigma^2 = 488.4$) than in those of females ($\sigma^2 = 1339.6$). Female occupied roost trees

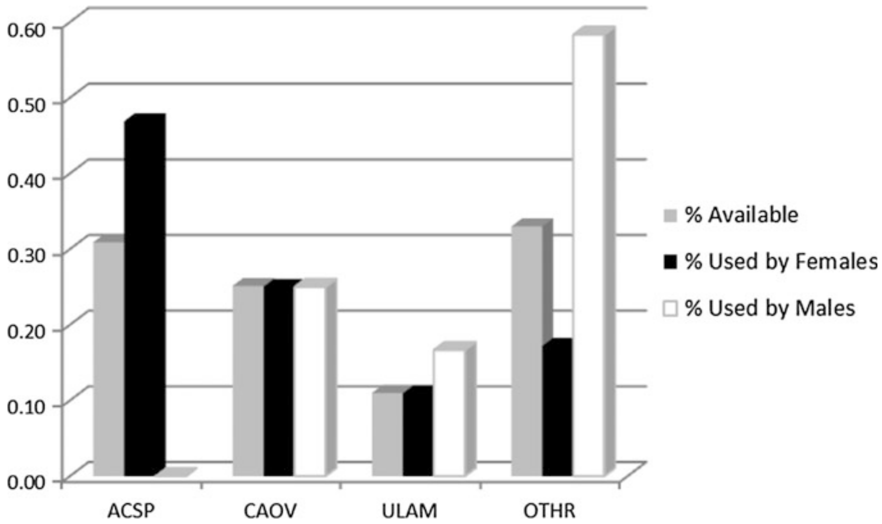

Fig. 2.3 Proportional use of roost tree species by male and female Indiana bats compared with available trees species in central New York State, 2006–2008. ACSP-*Acer* spp.; CAOV-*Carya ovata*; ULAM-*Ulmus americana*; OTHR-Other tree species

had a mean DBH of 41.75 ± 4.85 cm, and a mean height of 17.02 ± 0.73 m ($n = 57$) whereas male occupied roost trees had a mean DBH of 51.88 ± 6.38 cm and a mean height of 18.65 ± 1.46 m ($n = 12$). Separating roost trees by species and size classes (10–20; 20–30; 30–40, and 40+ cm DBH) revealed that bats selected *Ulmus americana* and *Acer* species size classes in proportion to their availability (*Acer* species: $G_{\mathrm{adj}} = 1.52$, df = 3; $P = 0.68$; *Ulmus americana*: $G_{\mathrm{adj}} = 5.17$, df = 3; $P = 0.16$), but that *Carya ovata* roost trees were selected at larger sizes (40+ cm DBH) (*Carya ovata*: $G_{\mathrm{adj}} = 8.73$, df = 3; $P = 0.03$).

While males and females selected similar diameter trees, they did show differences in the distribution of tree species selected for roosts (Fig. 2.3). *Acer* species made up 31 % of available trees, but represented 47 % of female roost trees and were not represented at all among male roost trees. *Carya ovata* made up 25 % of available trees, and were selected by both sexes in proportion to that availablity. *Ulmus americana* made up 11 % of available trees, and were selected by females in proportion to their availability, but males selected them more frequently (17 %). Other species collectively made up 33 % of available trees, but females selected from these only 17 % of their roosts, while males selected other species for 58 % of their roosts (females: $G_{\mathrm{adj}} = 7.77$, df = 3, $P = 0.05$; males: $G_{\mathrm{adj}} = 7.68$, df = 3, $P = 0.05$).

11.4 Discussion

This study suggests that Indiana bats are largely opportunistic in their selection of roosts, using roost resources largely in proportion to what is available to them in the landscape, at least based on the metrics measured. The species distribution of bat-selected roosts differed regionally, probably due to regional variation in the abundance and distribution of tree species, and therefore on availability (Luensman 2005; Kurta 2004), but also probably suggests a regional preference for species that provide suitable roosting conditions. Indiana bats in this study area used *Acer* species, *Carya ovata* and *Ulmus americana* most frequently, but only used *Acer* species and *Ulmus americana* more frequently than indicated by their availability, suggesting that these species are preferred species for this region. While *Carya ovata* was also used frequently, it was found to be used in proportion to its availability, so no preference for this species was indicated. Fewer roosts were found in *Quercus bicolor*, and *Salix nigra*, but each roost tree of these species was used multiple times, suggesting that these species may also provide a condition or resource preferred by Indiana bats.

Roost tree metrics recorded in this study are similar to findings from other studies conducted in the northern extent of the Indiana bat's range (Britzke et al. 2006 for New York and Vermont; Kurta et al. 2002 for Michigan), but smaller than those measured in the Midwest U.S. and core of the species' range, although such differences might be accounted for by the difference in tree species used by the bats (Kurta 2004). A comparison of roost metrics from several studies is outlined in Table 2.2. The three dominant roost trees from this study differ by at least one species from the most frequently used species in each of the other regions (Table 2.2). Dominant roost tree species in Missouri (Callahan et al. 1997) included

Table 2.2 Comparison of roost tree metrics from the Ontario Lake Plain of New York with those from similar studies in other parts of the Indiana bat's range

Metric	This study (2012)	Callahan et al. (1997)	Kurta et al. (2002)	Ford et al. (2002)	Britzke et al. (2006)
Location	New York	Missouri	Michigan	West Virginia	Vermont
DBH (cm)	41.6 ± 7.5	58.4 ± 4.5	42 ± 4	60.9 ± 7.7	45.6 ± 4.0
Ht of tree (m)	18.3 ± 1.4	–	18 ± 3	29.4 ± 2.0	18.9 ± 1.1
Ht of roost (m)	10.1 ± 1.5	–	10 ± 1	–	–
Most frequent species	*Acer spp.* *Carya ovata* *Ulmus americana*	*Quercus rubra* *Quercus alba* *Carya ovata*	*Acer spp.* *Ulmus americana* *Fraxinus nigra*	*Carya ovata* *Acer spp.*	*Carya ovata* *Populus deltoides* *Ulmus americana*
Live/dead	31 %/69 %	18 %/72 %	–	–	36 %/64 %
Bark/crevice	89 %/11 %	–	84 %/16 %	–	94 %/6 %

Quercus rubra and *Q. alba*; in Michigan (Kurta et al. 2002) included *Fraxinus nigra*; and in West Virginia (Ford et al. 2002) lacked *Ulmus americana*. The selection of roost trees by Indiana bats in central New York even differed in species distribution from those in the nearby Champlain Valley of New York and Vermont (Britzke et al. 2006; Watrous et al. 2006), where *Populus deltoides* was one of the three most frequently used species.

Most (90 %) roosts were under loose or protruding plates of tree bark, rather than in cracks or crevices in tree limbs or trunks. Of the three most frequently used tree species, *Acer* species and *Ulmus americana* both produce relatively large pieces of exfoliating bark on their snags compared to other tree species used, and mature live *Carya ovata* produce numerous pieces of exfoliating bark as part of their natural growth habit. This explains why *Acer* species and *Ulmus americana* were selected primarily as snags, but *Carya ovata* was typically used as a live tree, and in a mature growth state (DBH > 40 cm), which is about the size at which I observed the species beginning to exhibit exfoliating bark. Most (67 %) crevice roosts were found in *Acer* species. McComb and Muller (1983) suggested that *Acer rubrum*, which made up most of the Acer species in this study area, are particularly prone to cavity formation due to their susceptibility to fungal heart rots, and therefore are prone to provide potential cavity roosts for bats.

Roost tree sizes (DBH and height) in central New York were similar to those found by Britzke et al. (2006) and Watrous et al. (2006) in the Champlain Valley of New York, and similar to or smaller in both DBH and height than those found in other parts of the Indiana bat's range, as indicated in Table 2.2 (Kurta et al. 1993; Callahan et al. 1997; Foster and Kurta 1999; Ford et al. 2002). Whereas USFWS (2007) reported that males accept small diameter trees more often than do females, resulting in a smaller average DBH for male roost trees, male roost trees in central New York had a larger mean DBH (51.88 ± 6.38 cm) than those of females (mean DBH = 41.76 ± 4.85 cm). Male roost trees also had smaller variance ($\sigma^2 = 488.4$) than those of females ($\sigma^2 = 1339.6$), even though female roost trees had a larger sample size ($N_{\text{females}} = 57$; $N_{\text{males}} = 12$), which contradicts Barclay and Kurta's (2007) assertion that males generally use a wider range of roosting situations than females.

Of the most frequently used roost tree species, both sexes of Indiana bats used *Carya ovata* equally as frequently, and in proportion to their availability, suggesting opportunistic use. *Acer* species, however, were used by female bats far more frequently than their availability would suggest, while males did not use them at all. The strong female preference for this species suggests that it may provide important conditions for maternity colonies in the study area. Males tended to use *Ulmus americana* and other species more than their availability would suggest, while females used *Ulmus americana* proportional to its availability, and other species much less than their availability would suggest. These usage patterns suggest that males and females may select roosts to avoid intraspecific roost resource competition, or simply that each sex has different roost condition needs.

Woodlots in the Ontario Lake Plain of New York may be considered suitable habitat for Indiana bats if they contain snags of almost any size with exfoliating bark, but particularly maple or elm, or live or dead shagbark hickories of more than 40 cm DBH. Habitats dominated by maple snags may be considered more valuable for female Indiana bats and their maternity colonies, as they are selected preferentially by females, though woodlots with large numbers of *Carya ovata* or *Ulmus americana* may also be valuable, as they are used in proportion to availability. Females use other tree species much less frequently than their availability would suggest. Woodlots that are not dominated by maples, or do not contain *Carya ovata* or *Ulmus americana*, but contain snags of other species may still be valuable roost sites for male Indiana bats.

Whereas male roosts have not been considered a limiting factor on Indiana bat populations up to now, male roost tree size in this study area had a lower variance than those of females, suggesting that males may be more selective of roosts than females in this region. Wildlife managers and land use planners can use these traits to identify trees that might potentially provide suitable roost habitat for Indiana bats, and identify such trees for conservation to contribute to the possible recovery of this endangered species.

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Chapter 12
Effects of Range, Habitat and Roosting Ecology in Patterns of Group Association in Bats

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Abstract There is a wide variety of ecological factors that can potentially act as selective pressures driving the evolution of social behavior in bats. For instance, many behavioral ecologists recognize a relationship between social behavior, geographic distribution, and variation in resource abundance and distribution. Moreover, some bat species can use preexisting roosts such as tree cavities and caves, while others are able to modify nests, burrows, or foliage to create their own shelters. Thus, it is not surprising that the diverse social interactions found in bats have also been attributed to lifespan, availability, and distribution of roost sites. Here, I aim to determine if roost lifespan, number of roosts used and/or range size are important determinants of group stability. I conducted a literature review to collect information on group stability, roost lifespan, number or roosts used and range size, and I tested for correlated evolution between these variables. I found that roost lifespan, number of roosts and range size did not predict group stability. However, there was an association between range size and number of roosts used. Species with wider ranges encounter diverse habitats, environmental conditions, and roost types with different lifespans. Thus, it is not surprising that bats modify their social structure to adapt to these specific local conditions. Studying how different ecological characteristics interact to produce differences in group stability, provide the basis for understanding the complex route to sociality.

12.1 Introduction

Group living can result in a number of benefits, namely, reduced predation (Taborsky 1984; Hill and Dunbar 1998), increased foraging efficiency (Yip et al. 2008; Jarvis et al. 1994), better access to mates, efficient thermoregulation (Ancel et al. 1997), and potential cooperation (Black and Owen 1989; Silk et al. 2003;

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Cameron et al. 2009). However, it also has associated costs, including increased conspicuousness, resulting in increased predation risk (Wrangham and Rubenstein 1986), increased competition for limited resources and higher probability of disease transmission between group members (Wrangham and Rubenstein 1986). Animal aggregations can vary in size, composition, and stability in response to the environment. Factors such as resource availability and fluctuation can directly affect competition and hence influence the number of group members, the time they remain together, etc., (i.e., Emlen and Oring 1977; Sagot and Stevens 2012).

Social behaviors can evolve in species that live in groups (Alexander 1974). By developing social interactions, individuals enhance original advantages of group living, such as predator avoidance, efficient foraging, reduced parasite transmission, and reproductive competition (Alexander 1974). These behaviors can facilitate cooperative and mutualistic interactions among group members, which are key factors in formation of stable social groups (Alexander 1974). Bats are a particularly fascinating group of animals to examine how different ecological factors influence group living and social interactions, as the vast majority of species are social. Additionally, their social structure can vary widely within species. That is the case of Peter's tent-roosting bats (*Uroderma bilobatum*), where group size and stability vary according to roost types and habitat characteristics (Sagot et al. 2013, 2016, accepted). Moreover, bats exhibit a wide variation in mating systems including year-round harems with stable group composition (e.g., *Phyllostomus hastatus*; McCracken and Bradbury 1977), year-round harems with less stable group of females (e.g., *Carollia perspicillata*; Williams 1986), seasonal single male/multi-female groups (e.g., *Pipistrellus pipistrellus*; Gerrell and Lundberg 1985), seasonal multi-male/multi-female polygynous groups (e.g., *Tadarida brasilensis*; Cockrum 1969), year-round multi-male/multi-female groups (e.g., *Desmodus rotundus*; Wilkinson 1985) and single male/single female groups (e.g., *Vampyrum spectrum*; Vehrencamp et al. 1977).

The gregarious behavior and diverse social interactions found in bats have been in large part attributed to limited availability roost sites (Kerth 2008; Chaverri 2010). This is because roosts not only provide protection from predators and inclement weather (Ferrara and Leberg 2005; Lausen and Barclay 2006), but also play a central role in facilitating social interactions among conspecifics (Wilkinson 1986; Kerth et al. 2003; Chaverri and Kunz 2006; Ortega and Maldonado 2006). Bats use a wide variety of permanent (i.e., caves and buildings) and ephemeral (i.e., foliage) structures as roosts. Thus, one important feature of roosts that may affect social interactions is its longevity, or "lifespan". Indeed, Sagot and Stevens (2012) found that tent-roosting bats species using roosts of short lifespan, exhibited greater group stability compared to species roosting in long-lasting roosts. However, their work was performed only in tent-roosting bats, a group of bats species was able to build their own roosts (Kunz and Lumsden 2003). Species that lack this capability, but instead rely on environmental availability of resources, might also be affected by other ecological parameters such as habitat and range. This is because resources (such as food, water, and roosts) do not occur randomly in space. Therefore, many behavioral ecologists have long recognized a relationship between social behavior, geographic distribution, and variation of resources at different habitats (Johnson et al. 2002; Clutton-Brock and Harvey 1977; Horn 1968; Bradbury and Vehrencamp 1976; Crook 1964). That is the case of golden jackals (*Canis aureus*), which form stable and cooperative social groups in areas where feeding sites are limited, and loose aggregations in other ecological circumstances (MacDonald 1983). In bats, species inhabiting multiple habitats, commonly use multiple roosts types at different localities, as different roost types can be habitat specific (Sagot and Chaverri 2015). Since differences in habitat and resources can affect group living, it is possible that bats species utilizing multiple roost types at different habitats exhibit variation in their social structure. However, these ideas have not been addressed in detail. Furthermore, recent studies on a wide array of taxa have provided evidence that intraspecific geographic variation in behavior is common, especially in species with wide geographical ranges (Foster 1999). That is the case of the red fox (*Vulpes vulpes*) in which populations living in American prairies, form pairs in large territories; in Oxford, UK, they form groups in small territories; while in the taiga forests of Sweden, groups size vary with vole abundance (MacDonald 1983). Here, I aim to expand on Sagot and Stevens (2012) work, including 58 species, the vast majority of which do not build their own roosts. If roost lifespan is an important determinant of group stability, I expect a correlated evolution between roost lifespan and group stability. On the other hand, if patterns of geographic distribution and number of roosts used are important determinants of group stability, I expect to find an association between species range size and roost types with group stability. Identifying broad ecological factors affecting social structure and group stability across multiple bat species will deepen our understanding on the multiple routes to sociality.

12.2 Methods

I collected information on group stability and associated information on roosting ecology (i.e., number of roosts and roost type used per species), through literature searches on the Web of Knowledge (March 2014), using species scientific name, social system, roosts, and roosting ecology as keywords. I classified the mating systems proposed by McCracken and Wilkinson (2000), into binary discrete characters. The specific characters were (1) stable: groups found roosting together in a given roost for at least one reproductive season and (2) unstable: group association lasting less than a reproductive season. Roost lifespan was also coded into binary discrete characters based on the length of time a structure remained suitable for roosting. A roost was considered ephemeral if it was suitable for one bat generation or less (e.g., foliage roosts) or permanent if the structure persisted for multiple bat generations. To determine the effects of habitat, I categorized each species based on their geographical biome (tropical, subtropical, and temperate). This information was obtained from the IUCN Red List of Threatened Species (IUCN 2013). I also classified species range sizes in five categories: (1) 1–50 km^2; (2) 51.000–100 km^2; (3) 101–500 km^2; (4) 501–20,000 km^2; (5) 21,000–43,000 km^2) based on Sagot and Chaverri 2015.

To test for correlated evolution between roost lifespan and group stability, I implemented the DISCRETE module of Bayestraits (Pagel 1997), using Fritz et al. (2009) supertree, trimmed to comprise selected taxa (polytomies were arbitrarily resolved in Mesquite (Madison and Madison 2015), using the random polytomy resolution function. DISCRETE applies a continuous time Markov model to fit data to two maximum likelihood models: (1) a model of independent evolution, where the two traits evolve independently, and (2) a model of correlated evolution, where the two traits are correlated throughout the branch length. The test returns a log-likelihood (lnL) for both models, which is then evaluated using a Likelihood Ratio, LR = 2(log-likelihood(correlated model)–log-likelihood(Independent model)). This LR value is usually distributed as a chi-square with 4 degrees of freedom (Pagel 1994). Thus, a LR ≥ 4 is conventionally considered evidence that one model explains data significantly better than the other (Pagel 1999). Moreover, to estimate the effect of range size on number of roost types, considering the phylogenetic relationships among species, I performed Generalized Estimating Equations (GEE), using the function compar.gee, in the R package ape (Paradis et al. 2004). GEE was also used to determine if there is a correlated evolution between the number of roost types and range size on group stability.

12.3 Results

I obtained data for 58 species (11 families and 34 genera) distributed worldwide (Table 12.1). The correlated evolution analysis showed that roost lifespan and group stability evolved independently across the phylogeny (LnL independent model = −57.746; LnL correlated model = −58.287; $\chi^2_4 = 1.09$, $P > 0.05$). Eighteen species were reported to roost exclusively on ephemeral structures, while 28 used permanent roosts. Multiple species included in the analyses used more than one roost type. Thirty-three species were found in two or more roost types (ranging from 2 to 7), twelve of which were found roosting in both ephemeral and permanent roosts. Overall, there was no association between group stability and the number of roost types used ($T = -0.741$, dfp = 21.749, $P = 0.466$; Table 12.2).

There was no correlated evolution between group stability and range size ($T = 0.022$, dfp = 21.749, $P = 0.982$). Moreover, species with a tropical distribution showed extensive variation in both roosting ecology and group stability patterns. In contrast, subtropical and temperate species were reported to roost mainly in permanent roosts with no clear trend in patterns of group stability. However,

Table 12.1 Classification of group stability, number of ephemeral and permanent roost used and geographic distribution per bat species

Species	Group stability	Number of ephemeral roosts	Number of permanent roosts	Geographic distribution
Antrozous pallidus	Unstable	0	4	Temperate
Artibeus jamaicensis	Unstable	1	4	Tropical
Balantiopteryx plicata	Stable	0	5	Tropical
Barbastella barbastellus	Unstable	1	2	Temperate
Brachyphylla cavernarum	Stable	1	3	Tropical
Chalinolobus tuberculatus	Unstable	1	3	Temperate
Cynopterus brachyotis	Stable	1	0	Tropical
Dermanura anderseni	Unstable	1	0	Tropical
Dermanura cinerea	Unstable	1	0	Tropical
Dermanura phaeotis	Unstable	1	0	Tropical
Ectophylla alba	Stable	1	0	Tropical
Emballonura semicaudata	Unstable	1	1	Temperate
Eptesicus fuscus	Stable	0	4	Tropical/subtropical/temperate
Glossophaga soricina	Stable	0	3	Tropical
Hipposideros commersoni	Stable	1	2	Tropical
Hypsignathus monstrosus	Unstable	0	1	Subtropical
Latidens salimalii	Stable	1	0	Tropical
Leptonycteris curasoae	Stable	0	1	Tropical
Leptonycteris nivalis	Stable	0	3	Tropical/subtropical
Lophostoma brasiliense	Stable	1	0	Tropical
Macroderma gigas	Stable	0	2	Tropical

(continued)

Table 12.1 (continued)

Species	Group stability	Number of ephemeral roosts	Number of permanent roosts	Geographic distribution
Miniopterus schreibersi	Unstable	0	2	Tropical
Myotis bechsteini	Stable	0	3	Temperate
Myotis californicus	Unstable	1	4	Subtropical/temperate
Myotis capaccinii	Unstable	0	1	Temperate
Myotis evotis	Stable	1	4	Temperate
Myotis grisescens	Stable	0	1	Temperate
Myotis lucifugus	Stable	0	4	Temperate
Myotis nattereri	Stable	0	4	Temperate
Myotis sodalis	Unstable	1	2	Temperate
Myotis welwitschii	Unstable	2	3	Tropical
Mystacina tuberculata	Unstable	0	2	Temperate
Noctilio albiventris	Unstable	0	1	Tropical
Nyctalus lasiopterus	Unstable	0	3	Temperate
Nyctalus noctula	Stable	0	4	Temperate
Nycteris grandis	Stable	0	3	Tropical
Otomops martiensseni	Stable	0	2	Tropical
Pipistrellus hesperus	Unstable	0	4	Temperate
Pipistrellus nanus	Unstable	4	3	Tropical
Pipistrellus nathusii	Stable	1	4	Temperate
Pipistrellus pipistrellus	Unstable	0	4	Temperate
Plecotus auritus	Stable	0	3	Temperate
Plecotus mexicanus	Stable	0	1	Subtropical
Plecotus rafinesquii	Unstable	1	2	Subtropical
Pteropus livingstonii	Stable	1	0	Tropical

(continued)

Table 12.1 (continued)

Species	Group stability	Number of ephemeral roosts	Number of permanent roosts	Geographic distribution
Pteropus mariannus	Unstable	1	0	Tropical
Pteropus poliocephalus	Unstable	1	0	Tropical
Pteropus tonganus	Stable	1	0	Tropical
Pteropus vampyrus	Stable	1	0	Tropical
Rhinolophus sedulus	Stable	0	1	Tropical
Rhinophylla pumilio	Unstable	1	0	Tropical
Rhynchonycteris naso	Stable	1	5	Tropical
Saccopteryx leptura	Stable	0	1	Tropical
Uroderma bilobatum	Unstable	1	0	Tropical
Uroderma magnirostrum	Unstable	1	0	Tropical
Vampyressa nymphaea	Stable	1	0	Tropical
Vampyrum spectrum	Stable	1	0	Tropical
Vespertilio murinus	Stable	0	4	Temperate

Table 12.2 Percentage of species that exhibit stable or unstable social systems when using ephemeral, permanent or both types of roosts

Ephemeral		Permanent		Both	
Stable	Unstable	Stable	Unstable	Stable	Unstable
15.5	15.5	31.01	17.24	6.89	13.79

I found correlated evolution between the number of roost types and range size. I determined that species with relatively small range sizes used less roost types, compared to species with larger range sizes ($T = 2.102$, dfp = 21.749, $P = 0.043$; Fig. 12.1).

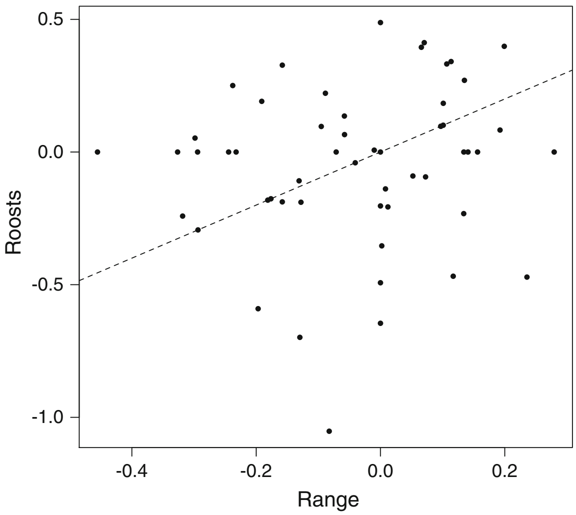

Fig. 12.1 Regression between phylogenetic independent contrast values for the number of roost types and range size

12.4 Discussion

The main purpose of this study was to determine whether group stability in bats could be predicted by roost lifespan or by other ecological parameters such as range size and roosts types, as a proxy of differences in habitat use. I sought to expand on previous evidence suggesting that the need of constant roost search when using roosts of short lifespan results in social stability among tent-roosting bats. In contrast to these findings, I found that roost lifespan does not predict group stability among the species included in the analyses. These two characters varied widely throughout the branch length. These results suggest that potential benefits of social grouping in response to spatial patterns in roost distribution are species and context specific. I discuss these findings based on the observed variability in roosting ecology and social systems.

12.4.1 Habitat Effects on Group Stability

In this study, I found that group stability and roost lifespan are not correlated across the phylogeny of 58 bats species, inhabiting different habitats. It is well known that resource availability is habitat dependent and patterns of resource abundance, diversity, and dispersion can explain group living (Johnson et al. 2002). For instance, habitats that provide high resource abundance often result in higher animal densities (i.e., Reiss 1988; Powell et al. 1997). In this context, multiple individuals can exploit resources over a common area without the detrimental costs that arise from gregarious behavior. Thus, it is not surprising that differences in availability of roost types found at different habitats, can influence patterns of group association even within species. For example, in the Peter's tent-roosting bat there is a correlation between population density and group stability with respect to distribution and abundance of the preferable roost type (the coconut palm, *Cocos nucifera*; Sagot et al. 2013, 2016 *in review*). Furthermore, distribution and abundance of resources also determine the ability of individuals to gain access to mates. For instance, harem holding males are typically able to defend the roost or a position within the roost they occupy. If roosts and thus, males are clumped in space and time, females are able to sample, and potentially mate with multiple males, decreasing group stability. This is the case of species such as *Cynopterus brachyotis* Sunda and *C. sphinx* (Storz et al. 2000a, b; Gopukumar et al. 2005; Campbell et al. 2006). When *C. brachyotis* Sunda roosts in coconut palms, which are highly abundant and clumped, group size, and composition are highly labile (Campbell 2008). In contrast, populations roosting in fan palms (*Corypha utan*), distributed in open landscapes, show more stable group sizes (Campbell 2008). Seasonality in availability of ephemeral roosts can also affect group stability. For example, *C. Sphix* commonly roosts in the highly clumped kitul palm (*Caryota urens*), which is available year-round (Storz et al. 2000b). Although this bat is able to use other plant species, alternative foliage roosts are not available during the dry season. Thus, at this time a year, harem groups become larger and males experience an increased potential for polygyny (Storz et al. 2000b).

Another reason for why groups stability varied widely throughout the branch length, might be related to intraspecific variation in group associations when inhabiting different habitats in wide geographic areas. Plasticity in social structure in response to differences in habitat and roost use has been documented in multiple mammalian species such as the bottlenose dolphins. In these species, intraspecific variation in social and genetic structure is attributed to habitat differences between sheltered near shore regions versus open coastline or offshore regions (Ballance 1992; Gowans et al. 2008). Moreover, primates and ungulates that live in complex habitats such as forests are often solitary or form small social groups, whereas those in less complex, open habitats, form comparatively larger groups (Crook and Gartlan 1966; Jarman 1974; Janson and Goldsmith 1995). In this case, formation of large groups in habitats characterized by patchy food and shelter availability facilitates food acquisition and predator avoidance (Wrangham 1980; Pulliam and Caraco 1984; Noë and Bshary 1997). This is also the case in *U. bilobatum*, where group stability varies according to the distribution and abundance of coconut palms (Sagot et al. 2013, 2016 *in review*).

In this study I found that bats with wider ranges commonly use multiple roosts types. This is not surprising, as different roost types, especially foliage roosts, are habitat specific. Moreover, larger geographic areas usually encompass distinct habitats and/or environmental conditions. Thus, if bats exhibit behavioral plasticity associated to differential habitat and roost use, as evidenced by multiple mammalian species, it is not surprising to find within species differences in the social structure and stability in response to differences in roost types.

12.4.2 Is Roost Lifespan Important?

Although Sagot and Stevens (2012) found correlated evolution between group stability and roost lifespan in tent-roosting bats, their hypothesis was not supported when including species that rely on environmental availability of roosts. Each tent-roosting bat species can only build their roosts in specific plants, as they depend on leaf shape for tent construction (Kunz and Lumsden 2003). Because of the restrictive number of plant species available to them, tent-roosting bats are more limited by roost availability, compared to other foliage-roosting bat species. In contrast, because plants are more abundant in nature than permanent structures such as caves and tree holes, tent-roosting bats are less limited than species that use permanent roosts. Thus, ecological and environmental parameters determining group stability, might be acting differently in tent-roosting bats, compare to other bats species.

Additionally, phylogenetic methods have difficulty detecting more than one change in a trait between nodes (Olson et al. 2009). Sagot and Stevens (2012) did not find a temporal order in the evolution of characters across the phylogeny, suggesting that changes in group stability and use of roosts of different lifespans might have occurred multiple times simultaneously throughout single branches, on ecological times scales, without been detected by phylogenetic methods. Thus, changes in group stability in tent-roosting bats seem to be influenced by plant availability and can change rapidly and even multiple times across a phylogenetic branch, creating unique patterns of group stability with respect to other bat species.

12.4.3 Biases in Studies of Social and Mating Systems in Bats

An issue with datasets as the one gathered for this study is that they rely on published information on mating and social systems. Studies describing grouping patterns included in our analyses were primarily conducted during the reproductive season. However, social behavior, particularly among female groups, might vary between reproductive and non-reproductive periods. For instance, the Mexican free-tailed bat (*Tadarida brasiliensis*) roosts in maternity colonies throughout the breeding season. However, a study comparing breeding colonies that use two different migration routes and their wintering colonies did not reveal distinct genetic differentiation, suggesting that females from the same maternity colony do not migrate to the same wintering colony, and thus, reflecting different group composition between seasons (McCracken et al. 1994).

Another challenge associated with studying free-ranging animals, in particular nocturnal species, is that social behavior is commonly described based on a limited number of populations. The social systems of these species are thus commonly classified as “species-typical” and are considered invariant within species (Foster

1999). Moreover, although multiple studies have shown geographic variation in numerous genetic and phenotypic traits (Endler 1992; Foster and Endler 1999), studies addressing geographic variation in behavior are relatively scarce (Foster 1999).

12.5 Conclusions

Here I presented evidence suggesting patterns of group stability are associated to differences in roost use. Species inhabiting wider geographical ranges encounter diverse habitats, environmental conditions, and roost types with different lifespans. Because different roost types at different habitats provide different conditions (size, duration, exposure to predators, thermoregulation, etc.), it is not surprising that bats are able to modify their social structure to adapt to these specific local conditions. Studying how different ecological characteristics interact to produce differences in group stability, provide the basis for understanding the complex route to sociality.

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Chapter 13
Responses of Bat Social Groups to Roost Loss: More Questions Than Answers

Alexander Silvis, Nicole Abaid, W. Mark Ford and Eric R. Britzke

Abstract Though characterization of, and understanding determinants of, social structure in bats is increasing, little is known about how bat social groups respond to disturbance resulting in roost loss. Given that many species of bats roost in ephemeral or transitory resources such as plants, it is clear that bat social groups can tolerate some level of roost loss. Understanding responses of bat social groups to roost loss can provide insight into social structure that have applied conservation use. Herein, we review the existing literature on the effects of disturbance on bat social groups, and present a parameterizable agent-based model that can be used to explore the relationships among roost dynamics, population dynamics, and social behavior.

13.1 Introduction

Disturbance can have substantial impacts on the current and future conditions of wildlife habitat that in turn can either impact animals directly or indirectly across a wide temporal scale. While there can be negative impacts on wildlife both for

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individual animals and larger populations, tolerance to disturbance, be it anthropogenic or natural, is important for persistence in dynamic habitats. This is particularly true as anthropogenically modified landscapes now dominate much of the Earth's surface. As disturbance regimes will likely increase in intensity in the future due to factors such as increased urbanization, climate change, and changes in land use, gaining a more complete understanding of the impacts of disturbance on wildlife is needed.

The relationship between habitat disturbance or modification and bats generally is poorly understood, with information spread unevenly among major taxa and habitat types. The majority of research on the topic has focused on the impacts of habitat disturbance and loss, with measurements of responses in bat home range size and configuration, foraging habitat use and day-roost selection, and overall site occupancy (Gorresen and Willig 2004; Henderson and Broders 2008; Henderson et al. 2008; Borkin and Parsons 2011; Ethier and Fahrig 2011; Bender et al. 2015). Understanding these broad areas of bat ecology is critical for habitat conservation measures, but these topics address only a limited aspect of the ecology of many species. As contributions in this book show, interest in bat social systems, and particularly in those with social structures not defined by mating hierarchies, is increasing. This increased research interest has revealed the presence of nonrandom social structure in numerous bat species Wilkinson (1985a, b; McWilliam 1988; Kozhurina 1993; McCracken and Wilkinson 2000; Popa-Lisseanu et al. 2008). There now is clear need for the study of social structure to be integrated into future studies on the impacts of habitat disturbance on bats.

At a very basic level, participation in a society comes with both costs and benefits. For bats, particularly those species that form colonies, group membership increases the potential for disease transmission, or otherwise imposes social costs [e.g., disadvantage due to conspecific cheating behavior (Carter and Wilkinson 2013a)]. In light of these costs, group membership must be counterbalanced by considerable net benefits [e.g., resource sharing, fitness (Carter and Wilkinson 2013b; Kilgour et al. 2013; Garg et al. 2015)]. It is natural therefore to consider the impacts of disturbance on sociality and/or social structure when assessing the impacts of disturbance on bats. Demographic parameters such as survival and recruitment often are difficult to collect for bats; understanding disturbance on social structure may yield important insight into these parameters.

Moreover, an understanding of the impacts of disturbance on bat social systems may also yield information on the mechanisms that allow bats to persist under disturbed environmental or social conditions. In this chapter, we review the issue of roost loss on bats, analytical approaches to understanding impacts of roost loss on bats, and empirical studies of roost loss impacts on bats. Further, we develop and present a paramaterizable agent-based model that can be used to prospectively or retroactively explore the relationship between roost dynamics, bat population dynamics, and bat social structure.

13.2 Review of the Literature

13.2.1 Bat Roosting Behavior

Understanding the impacts of roost loss on bats is not merely an academic issue. Habitat loss widely is considered to be one of the critical issues facing ecosystems and wildlife globally (Hoekstra et al. 2005; Mantyka-Pringle et al. 2012). Greater knowledge on the impacts of roost loss on bat social systems has clear implications for mitigation of adverse human impacts on bats, bat habitat, and proactive conservation work in multiuse landscapes. Worldwide, approximately half of all known bat species roost in plants (Kunz and Lumsden 2003). Although roost plants may persist for considerable time periods, e.g., furled leaves, trees, or snags, plant roosts are inherently ephemeral with “lifespans” ranging from days to decades (Cline et al. 1980; Moorman et al. 1999; Vanderwel et al. 2006). Similarly, other environmental limitations such as encroaching vegetation or occupancy by competitor species may render roosts unavailable for a portion of the total “lifespan” of the day-roost structure. How then do bats respond to roost loss? The response likely is correlated with the ephemerality of the roost. Loss of roosts that are more ephemeral likely has smaller impacts than loss of more stable roosts.

Social systems and roosting behavior of bats provide some insight into how bats may withstand roost loss. In particular, roost-switching behavior and the fission–fusion social dynamic found in numerous bat species (Kerth and Konig 1999; Willis and Brigham 2004; Garroway and Broders 2007; Rhodes 2007; Popa-Lisseanu et al. 2008) suggests that bats are cognizant of alternative roosts sites in the event of the loss of a single or small number of day-roosts. In this case, it may be relatively easy for bats to gradually shift roost use patterns around existing and newly located roosts. Anecdotal evidence suggests that bats may not be using all of the suitable roosts in an area at a given time (Silvis et al. 2014b). Alternatively, for bat species that are resource or habitat specialists, use limited numbers of roosts, or roost switch infrequently, roost loss may have higher consequences.

Theoretically, roost loss may impact or alter bat social structure and roosting behavior in a number of ways. Outside of a direct impact on individual members of the bat colony, alterations may be either an increase or decrease in social network structure. Because social networks may be mathematically described using a suite of descriptors [e.g., centralization, clustering, density, homophily, modularity, degree distribution, etc. (Boccaletti et al. 2006)], and because bat species differ greatly in their social ecology, it is difficult to succinctly summarize here what changes to individual metrics may suggest for different species. Broadly, however, increases in structure related to group closeness could suggest that the maximum benefits of group membership are needed, could indicate a division or reorganization of the group, or could result from a restricted number of available roosts. In contrast, decreases in group closeness could suggest the dissolution of a social group, or disruption of group dynamics. In any case, how other aspects of bat ecology alter in conjunction with social structure and environmental conditions, provide critical context for understanding changes in social structure. For example, decreased social structure in conjunction with increased space use by individuals, with substantially decreased roost availability, would support assertions of group dissolution.

13.2.2 Analytical Approaches to Understanding Roost Loss Impacts

Rhodes et al. (2006) were among the first to formally discuss the ability of bats to tolerate roost loss (Rhodes et al. 2006). In their discussion, Rhodes et al. (2006) constructed a day-roost network showing connections among roost trees given bat roost-switching movements by a maternity colony of white-striped free-tailed bats (*Tadarida australis*) in Australia. Based on the fit of a power law to the degree distribution of network nodes, Rhodes et al. (2006) described the network as scale-free, forming the basis of their discussion of the application of networks to understanding roost disturbance on bats. Scale-free networks are one of many network types, and particularly are known for their structural property of robustness to node "failure" (Albert et al. 2000; Wang et al. 2006; Ou and Yang 2012). The robustness of scale-free networks to node loss makes an attractive framework from which to assess the impacts of day-roost disturbance on bats, but treatment of networks as scale-free by researchers in a variety of fields has been criticized for several reasons. These include small sample size and inappropriate methods such as use of least-squares fitting to identify scale-free condition (Clauset et al. 2009; James et al. 2009). To demonstrate that a network has a power law degree distribution (and thus scale-free condition), rigorous model fitting and goodness of fit testing are required, along with considerable sample size (Clauset et al. 2009). Relative to the amount of data available for many bat species, robust determination of scale-free status may not be wholly feasible, and therefore consideration of roost and social networks as scale-free is inappropriate.

Even if day-roost networks cannot be classified as scale-free, network analysis provides a useful framework for understanding the impacts of day-roost loss on bats. Two-mode network analysis in particular (which partitions nodes representing bats and roosts) may be useful in evaluating the effects of day-roost loss, as the two-mode nature of the network allows visualization of how the loss of individual trees may disconnect sections of the bat or roost network (Silvis et al. 2014a, b). Furthermore, the single-mode network projections of the day-roost network from a two-mode bat roost network connects all nodes used by an individual bat, and can be used to determine whether the loss of a day-roost may remove an irreplaceable and important social center (Silvis et al. 2015). Similarly, single-mode projections of the social network of bats may be used to understand the impacts of loss of individuals from bat societies (Chaverri 2010).

13.2.3 Review of the Empirical Literature

Relatively few studies directly have studied the effects of disturbance on bats using pre/post- treatment impact assessments, and even fewer directly have investigated the impacts of disturbance on bat social systems, or the intersection of bat social systems, behavior, and habitat use. To our knowledge, only two studies have experimentally tested impacts of disturbance on bat social structure; both focused on the impacts of roost loss. Chaverri and Kunz (2011) artificially restricted access to roost plants used by Spix's disc-winged bat (*Thyroptera tricolor*) in Costa Rican tropical forests (Chaverri and Kunz 2011). Subsequent tracking of individuals revealed that social cohesion decreased while roosting home range increased. Silvis et al. (2015) artificially removed roosts used by maternity colonies of northern long-eared bats (*Myotis septentrionalis*) in a temperate hardwood forest in Kentucky, U.S.A. (Silvis et al. 2015). Roost use patterns following roost removal indicated potentially differential social responses to loss of primary and multiple secondary roosts, with indications of colony fragmentation following loss of multiple secondary roosts. In contrast, loss of a single primary roost appeared to have relatively little impact on the social structure of the colony (Silvis et al. 2015).

Whereas Chaverri and Kunz (2011) studied a roost specialist species, Silvis et al. (2015) studied a roost generalist species (Menzel et al. 2002; Ford et al. 2006; Perry and Thill, 2007). Although a sample size of two studies is too small to draw broad scale conclusions with strong inference, differences in response to roost loss between the species studied by Chaverri and Kunz (2011) and Silvis et al. (2015) are interesting and relatively consistent with what might be expected of the species based on roost selection specialization. In general, it seems likely that roost specialists, and/or those that switch roosts infrequently, may be more negatively impacted by roost loss than would roost generalists or those that use a number of roosts and switch frequently within the context of relative roost availability. Similarly, it seems plausible that bats that form maternity colonies distributed across a number of roosts, such as the Indiana bat (*Myotis sodalis*) (Silvis et al. 2014b), may be less impacted by roost loss, particularly if information on roost location and quality is shared among individuals (Kerth and Reckardt 2003; Jonker et al. 2010; Furmankiewicz et al. 2011; Clarin et al. 2014).

Three additional studies have used simulations to understand the potential impacts of disturbance on bats. Chaverri (2010) removed an increasing proportion of randomly selected individual bats from social networks of Spix's disc-winged bat, and recalculated network metrics (Chaverri 2010). The second and third, in (Silvis et al. 2014a, b), used a similar approach but with roosts rather than individual bats. The results of the simulations by Chaverri (2010) and Silvis et al. (2014a, b) suggest that loss of both individual bats and roosts results in nearly linear increases in the number of network components, i.e., social groups, which is highly suggestive of fragmentation of the social group. However, it is important to consider that the aforementioned random and targeted network roost-removal simulations above do not incorporate a number of important factors such as day-roost spatial arrangement, roost quality, or changes in individual behavior that may determine how social groups of bats respond to roost loss. Nonetheless, the results of the field roost-removal study by Silvis et al. (2015) generally were congruent with the earlier simulation-based predictions of Silvis et al. (2014a). Although roost loss was not directly tracked, in West Virginia, U.S.A., Johnson et al. (2012a) found that, in areas subjected to prescribed fire where some preferred day-roosts were lost and large numbers of usable, but less-preferred roosts were recruited (Ford et al. 2016), northern long-eared bats maintained maternity colonies with social dynamics similar to those in unaffected habitat (Garroway and Broders 2007).

13.2.4 More Questions Than Answers

The majority of studies on bat social structure have been descriptive, and are constrained by a lack of temporal data (throughout a season or across years), in the number of social units sampled, and geographic variation. Comparisons of observed social structures with equivalent random structures have proven useful for determining whether observed structures are chance results or due to specific processes, but do little to uncover the processes resulting in observed social structures or provide estimates of what may occur in the future under specific environmental/roosting conditions. Moreover, the (currently) small number of studies on bat sociality, and the absence of systematic sampling across either habitat types or taxa, makes it difficult to make many robust conclusions or conduct any systematic meta-analysis relating social group structure to habitat structure/condition. These studies have, however, highlighted the fact that there are more questions than answers when it comes to the responses of bats to roost loss.

Despite the concordance between observed and theoretical results presented above, with so few empirical studies, it is unfeasible to consider theoretical predictions robustly supported at this juncture, particularly when considering the hierarchical nature of the issue among and within taxa. At the broadest level, still it is unclear how responses to roost loss differ among bats with different social systems and roost specialization/selectivity, and by extension, what are the underlying mechanisms within each social structure that generates positive, neutral, or negative response to roost loss. At more local levels, it is unknown how response to roost loss differs among social groups of the same species within different habitat types, or how individual roost condition/quality at a site impacts the severity of the impact of roost loss. At the group level, little is known about temporal group dynamics, how timing of roost loss impacts social structure, and whether these factors may have reproductive consequences. What role social communication may play in mitigating the impacts of roost loss, and how social bonds among individual bats may facilitate group reformation after fragmentation, also currently is unknown, although at least one species of bat is known to emit social calls to recruit roost-mates (Chaverri and Gilliam in publication). To date, much of the research on the topic of habitat disturbance and bats has focused on broad scale impacts, such as effects on home range, habitat use and selection, and occupancy (Gorresen and Willig 2004; Henderson and Broders 2008; Henderson et al. 2008; Borkin and Parsons 2011; Ethier and Fahrig 2011; Bender et al. 2015). Indirectly, aspects of these investigations may provide insights into how bat social groups respond to roost loss. For example, changes in home range (Borkin and Parsons 2011) may suggest that social cohesion decreases, as observed by Chaverri and Kunz (2011). Field studies suggest that variation in social structure among groups of the same species may be common (Johnson et al. 2012b; Silvis et al. 2014a), and possibly related to ecological conditions such as roost availability (Chaverri 2010) or loss (Chaverri and Kunz 2011; Silvis et al. 2015). In cases where a modicum of information is available on social structure and behavior, understanding of the potential impacts of roost loss on bat social structure may be informed by reviewing impacts of habitat disturbance and loss on home range, space use, and habitat selection.

13.3 An Agent-based Model to Explore the Impacts of Roost Loss on Bat Social Structure

13.3.1 Why Agent-based Modeling

Understanding of the factors that cause or are correlated with social behavior and social dynamics in bats is expanding (Kerth 2008), but there currently is little predictive or prospective analysis, and no formal framework for creating predictive models of social structure relative to behavioral or environmental characteristics. Because many species of bats are highly social, studying the impacts of habitat alteration on bats requires an understanding of the interaction between social dynamics and resource selection. Agent-based (a.k.a. individual-based) modeling provides a tool that is useful for just such analyses (McLane et al. 2011). Agent-based models are widely used in a variety of fields. In ecological studies, agent-based models have been used to understand parasite and disease transmission (Bonnell et al. 2010; Nunn et al. 2011), generate management strategies (Conner et al. 2008), model energy budgets and foraging (Stillman 2008; Sibly et al. 2013), territoriality (Giuggioli et al. 2011), collective motion (Huth and Wissel 1992, 1994; Bode et al. 2011), and human impacts on natural systems (An 2012) and land use patterns (Bithell and Brasington 2009). Few studies have used agent-based models to understand social behavior in wildlife [but see (Giardina 2008)], although this modeling technique is common in studies of human social behavior (Gilbert and Terna 2000). In their pioneering work, Kashima et al. (2013) demonstrated that learning-based models can be used to successfully explore fission–fusion dynamics in bats relative to infection risk. In the following, we present an aspatial agent-based model for investigation of the effects of stochasticity in roosting resources on the fission–fusion dynamics of bat social groups in the context of bat population dynamics and changing resource suitability. We present both the model and an example using the northern long-eared bat.

13.3.2 Overview of Model

We consider a system comprising N bats and R roosts, where bats annually select a set of roosts under a set of roost lifecycle and bat population dynamics. The colony's dynamics are simulated for T years, where bat roosting data is sampled s times per year. During each year, we execute an agent-based model to dictate the bat roost selection at the s discrete time steps, which can be viewed as an annual roost selection cycle by the members of a maternity colony. In year k, the model updates an $(N \times s)$-dimensional state matrix called $x(k)$, whose ijth entry is the roost selected by bat i at sample j. The roost selection depends on the roost quality, which updates annually and is captured in the R-dimensional vector $Q(k)$. We note that the colony size and number of viable roosts is able to change dynamically, that is $R = R(k)$ and $N = N(k)$, and the bats' indices in the state vector are not necessarily retained over time; that is, $x_i(k)$ is not necessarily the updated roost selection of the same bat referred to be $x_i(k\text{-}1)$. The roost selection update depends on three dynamic processes: (i) roost creation/elimination and roost quality decay process, (ii) bat interaction with known conspecifics and random roost exploration, and (iii) bat natality and mortality. We discuss the implementation of each process in the model and summarize the steps in Fig. 13.1.

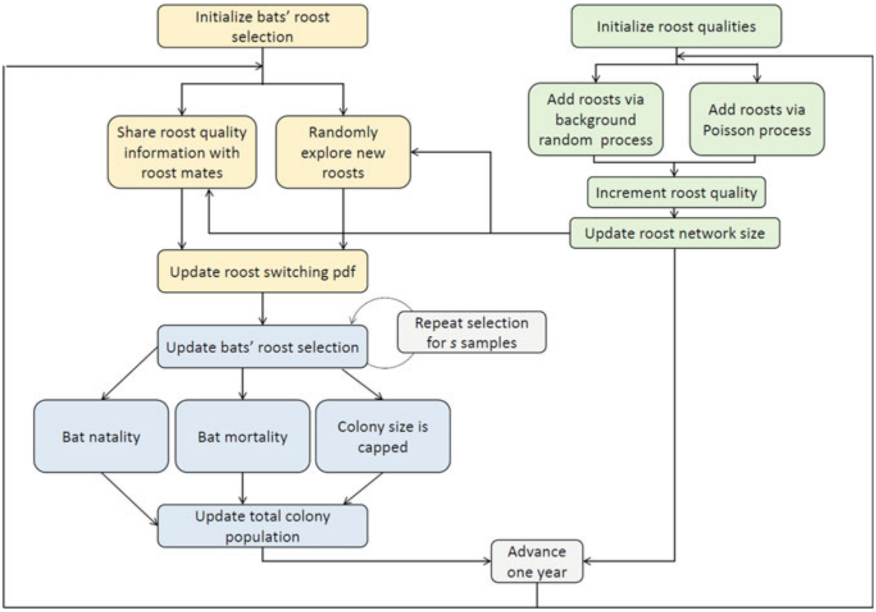

Fig. 13.1 Flow diagram of the agent-based model for bat roost selection across years relative to bat and roost dynamics. Note the sub-loop for repeat roost selection within years

13.3.3 Roost Creation and Elimination and Roost Quality Decay

An initial number of roosts R_{int} is selected for the colony. After initialization, roosts are introduced to the system via two mechanisms. First, roosts are created at each time step according to realizations of a random variable with a normal distribution with zero mean and variance v. In year k, the realization is generated, and the positive integer part taken as the number of new roosts from this process. Second, roosts are added according to realizations of a Poisson process (Parzen 1999) that is designed to simulate aperiodic and relatively infrequent disturbance events that cause tree mortality and thus introduce new roosts into the ecosystem, i.e., ice storms, wind damage, fire or insect attack. In year k, the number of new roosts from such events is the product of independent realizations of a Poisson random variable with parameter λ and a discrete random variable uniformly distributed in $[0, 2d]$.

Once roosts are created, their quality is initialized in [0, 1] and appreciated multiplicatively, that is, $Q(k + 1) = (1 + q)Q(k)$. The parameter q is a fixed appreciation factor in [0, 1]. When roost quality is provisionally updated as greater than one, it is reassigned as zero. This process is designed to model the lifecycle of the snags (standing dead trees) that bats use as roosts. Over time, the snags develop more cavity spaces where bats may roost, until the snag eventually decays to the point of collapse and is no longer used as a roost. In the model, roosts are permanently removed from use once their quality exceeds one.

13.3.4 Bat–Bat Interaction and Roost Exploration and Selection

In the model, bats select roosts from realizations of a probability mass function (pmf) determined by the quality of roosts to which they have access. Specifically, each bat is initialized with a uniformly distributed pmf, which is an R-dimensional vector, containing nonzero entries for r_{int} roosts (each equal to $1/r_{\text{int}}$) independently of the roost's quality. Bats are then randomly chosen to occupy one of these roosts for their first time step.

At successive time steps, bats select roosts based on realizations of the pmf, which is updated based on their previous pmf, information on roost quality shared among roost-mates, and information gathered by random roost exploration. We model the sharing of information on roost quality among roost-mates by computing a vector that condenses the information bat i receives from all peers during roost sharing, which we label

$$P_i^1(k) = \sum_{j \in R_i(k)} \sum_{b \in j} P_b(k) * Q(k)$$

where $*$ is the element-wise product of vectors and $R_i(k)$ is the set of unique roosts occupied by bat i during any of the samples at time k. Thus, when bat i occupies roost j during the same year as bat b (which we call sharing a roost), we compute bat b's pmf weighted by the true roost qualities; these weighted pmfs are summed over all bats in shared roosts. To capture roost quality information garnered by a bat's random exploration of the roost network, we select r_{ex} roosts uniformly from all the viable ($Q > 0$) roosts. Information about the roosts explored by bat i are gathered in a vector, $P_i^2(k)$, whose only nonzero entries are the qualities of the roosts randomly selected for exploration.

Then, the roost quality pmf at time $k + 1$ is updated for bat i at time k by the normalized weighted average

$$P_i(k+1) = \frac{(1-a-b)P_i(k) + aP_i^1(k) + bP_i^2(k)}{\| (1-a-b)P_i(k) + aP_i^1(k) + bP_i^2(k) \|_1}$$

where $\| v_1 \|$ is the 1-norm of vector v, which makes $P_i(k+1)$ have sum equal to one. A bat maintains this pmf for the entire annual time step and the s roost selection samples for $x_i(k + 1)$ are independent realizations of $P_i(k + 1)$.

13.3.5 Bat Natality and Mortality and Colony Size Limitation

We model the mortality–natality processes using two uniform random variables whose parameters are the mean bat survival and recruitment rates, respectively. Specifically, we define a Bernoulli random variable which equals one with probability b_s and zero otherwise; at each annual time step, independent realizations of this random variable are generated for each bat to determine if it survives a given year. Similarly, we define a Bernoulli random variable which equals one with probability b_r and zero otherwise; at each annual time step, independent realizations of this random variable are generated for each bat to determine if it recruits another single bat in a given year. Bats which do not survive a time step are randomly selected and removed from the state matrix in that year. Recruited bats have their initial pmfs defined analogously to the simulation initialization. Finally, since a set of roosts is only able to support a finite number of bats, we impose an upper limit on the colony size, which we define as $N_{\max}$, and we randomly remove bats to enforce that the total population does not exceed this limit.

13.4 Observables

13.4.1 Roost and Bat Population Dynamics

Since the roost network is viewed in the context of the bat colony it supports, we consider the overall survival or extirpation of the bat colony. The population size of the colony over 50 years is used to assess the colony robustness. Similarly, the survival of the roost network itself also acts as a salient variable for the bat colony robustness.

13.4.2 Clustering Metrics

We assess the bat population, their social interactions, and common roosts from a network perspective. The bat social network is built by considering each bat as a node and edges between bats as existing when bats reside in the same roost in a given year (i.e., the single-mode network of bat nodes derived from the two-mode network of bats and roosts). We consider networks to be undirected, since social interactions are in general symmetric. To quantitatively assess the social network, we examine three measures of network properties: the Morisita clustering index, the mean degree centralization, and the number of connected components. However, in practice, any desired network metric could be calculated from experimental data.

The Morisita index (Morisita 1959) measures aggregation of bats over the roost network at each annual time step. It is defined as

$$I(k) = \frac{1}{sN(k)(sN(k)-1)} \sum_{j=1}^{R(k)} p_j(k)\left(p_j(k)-1\right)$$

where the number of bats in roost j during all samples of year k is $p_j(k) = \sum_{i=1}^{N(k)} \delta_{x_i(k),j}$ and $\delta_{i,j}$ is the Kronecker delta function that equals one when $i = j$ and zero otherwise. The Morisita index is between zero and one; it equals one when all bats reside in a single roost during all samples and zero when all bats occupy roosts alone. Thus, higher values of $I(k)$ indicate that bats select more common roosts and lower numbers show more isolated roosts are selected.

The degree centralization (Freeman 1979) is taken as the mean degree of each bat in the roosting network, which is the number of links originating or terminated at that node, normalized by the total number of nodes in the network. To compute this quantity, we write an ($N(k) \times N(k)$) adjacency matrix whose ijth entry is one if there is an edge between bats i and j, and zero otherwise. The degree centrality is between zero and one; it equals one in an all-to-all graph and zero if all individuals are isolated. In general, higher values of degree centrality are for networks with larger number of connections.

In a network, a set of nodes is called connected if there exists a path of edges in the network that connects every pair of nodes. We want to measure the number of disjoint subsets comprising the bat social network whose bats only communicate within their subset of nodes; these subsets are called connected components of a network. The number of connected components in a graph is computed using the graph Laplacian, a matrix equal to the difference of the matrix with node degree on the diagonal and the adjacency matrix. Notice that graph Laplacian has zero row sum by definition, which means that it has at least one eigenvalue equal to zero. In linear algebra, the number of connected components in a network is equal to the algebraic multiplicity of the zero eigenvalue (Anderson and Morley 1985).

13.5 Case Study

As a case study, we explore whether bat social network structure (in terms of model observables) is dependent on roost dynamics under different population dynamics using a Monte Carlo approach that allows us to assess stability of our results over a number of stochastic model trials. Toward this goal, we fix most of the model's free parameters and only vary bat recruitment and survival parameters. For this case study, we used free parameter values that we believe are representative of the northern long-eared bat derived from a review of published information on social structure of this species (Garroway and Broders 2007; Johnson et al. 2012a; Silvis et al. 2014a, b). As a general overview, the northern long-eared bat is a temperate species that forms maternity colonies usually of ≤30 individuals in cavities or under the loose bark of trees/snags (Menzel et al. 2002; Carter and Feldhamer 2005; Silvis et al. 2015). Individuals within colonies switch roost every few days, with colonies displaying a fission–fusion social dynamic across roost networks of as many as 42 roosts; social connections appear to be temporally structured (Garroway and Broders 2007; Silvis et al. 2015). Colony roost networks tend to exhibit higher than random levels of degree centralization with "primary" and "secondary" roosts, where primary roosts are characterized by intense use and secondary roosts by limited use (Johnson et al. 2012a; Silvis et al. 2014a).

We initialize our case study network with 20 bats and 35 roosts and simulate the system response over $T = 50$ annual time steps using the parameter values in Table 13.1. The same realization of the roost dynamics is considered for simulations hereafter unless otherwise stated, and it is shown in Fig. 13.2. From Fig. 13.2a, we see that the number of viable roosts increases dramatically in years when the Poisson process has nonzero value, and gradually declines in years when there is no disturbance. This decline is due to the roosts' incremental increase of quality each year until exceeding one whereby they cross a condition threshold, cease to be usable, and are thus excluded from the model, shown in Fig. 13.2b. Given this roost dynamic, we compute five replicates of the simulation for two values of the bat recruitment parameter ($b_r = 0.3$ and 0.4) and bat survival

Table 13.1 Model parameters for simulation study of northern long-eared bat (*Myotis septentrionalis*) maternity colony networks

Parameter	Symbol	Value	Parameter	Symbol	Value
Annual time steps	T	50	Initial number of bats	N_{int}	20
Number of roost samples per year	S	5	Mean bat recruitment	b_r	0.3, 0.4
Initial number of roosts	R_{int}	35	Mean bat survival	b_s	0.7, 0.8
Roost depreciation factor	Q	0.1	Maximum colony population	$N_{\max}$	40
Variance of background roost add process	V	1	Initial number of roosts bats know	r_{int}	3
Poisson parameter for disturbances	Λ	0.1	Number of roosts explored per bat per year	r_{ex}	2
Mean number of roosts generated by disturbances	d	20	Peer weight 1 (peer)	A	0.8
			Peer weight 2 (rand)	b	0.1

parameter ($b_s = 0.7$ and 0.8). The results of these simulations are shown in Fig. 13.2c–f.

Comparing the number of bats when b_r and b_s are varied, we see that high values of the recruitment and survival parameters ensure a short initial transient and saturation of colony size at the maximum supportable population, seen in Fig. 13.2c. As the values of these parameters are decreased, the transient length increases, and when both b_r and b_s are both relatively small (0.3 and 0.7), the colony size never saturates and is even at risk of dying out. Moreover, the variance between replicates (seen in the size of error bars taken over the five replicates) is smaller during the initial transient when recruitment and survival are higher. However, trends in the bat population do not seem to correlate with variations in the roost dynamics.

On the other hand, the observables for the bat social network with varied b_r and b_s show a robust dependence on the roost dynamics and, interestingly, are relatively less sensitive to the bat population dynamics. For all three network metrics shown in Figs. 13.2d–f, we find high consistency between replicates (seen in small error bars over the replicates) and between parameter cases (seen in matching between curves with both values of b_r and b_s); this is in contrast to the lack of correspondence in the bat population time series as the bat survival and recruitment parameters are varied. In particular, we see that the Morisita index is high when only a small number of roosts are viable, for example near year 20; in this case, the bats are forced to cluster due to lack of roost selection options. The degree centrality shows a similar trend, since bats occupying common roosts means that more connections are built in the bat social network. The number of connected components shows an opposite trend, with values larger than one when large number of roosts are viable, in this case near years one and 25. In other words, when bats may select from many roosts, they are more likely to form disjoint subnetworks.

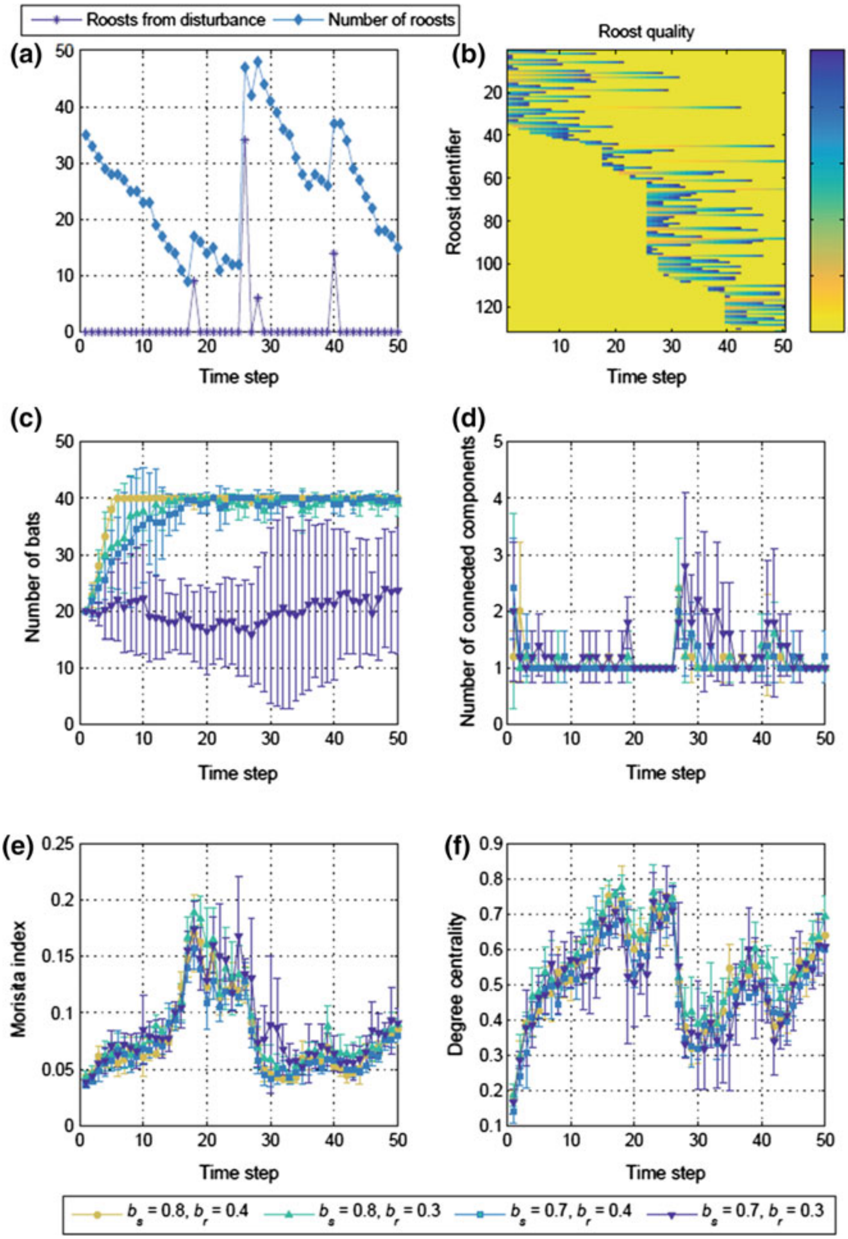

Fig. 13.2 Simulated roost dynamics showing **a** number of roosts added from disturbances and total number of viable roosts and **b** the time evolution of qualities for all roosts. Simulated bat population and social network dynamics in terms of **c** total number of bats, **d** number of connected components, **e** Morisita clustering index, and **f** degree centrality. Bat survival and recruitment are varied between simulations and error bars show one standard deviation over 5 replicate Monte Carlo simulations. All time steps are in years

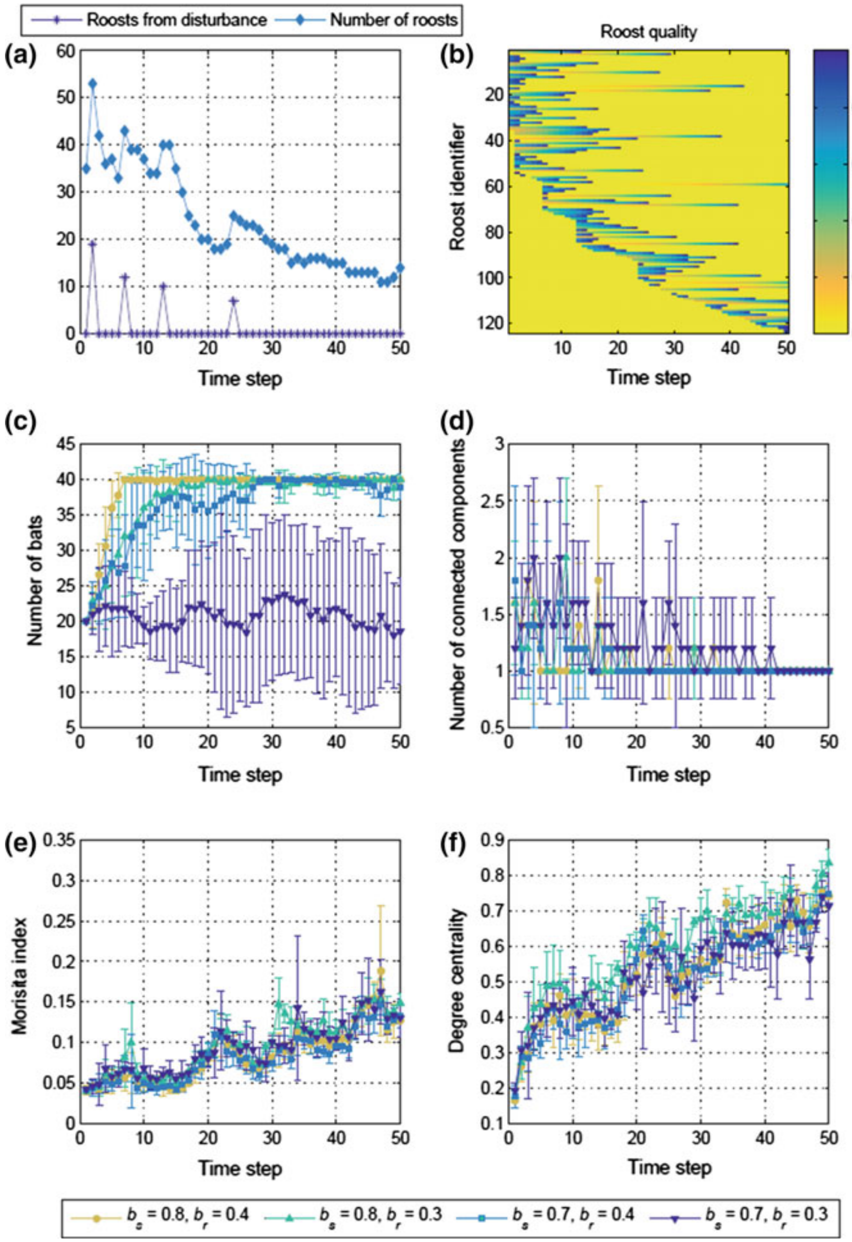

Fig. 13.3 Simulated alternative roost dynamics showing **a** number of roosts added from disturbances and total number of viable roosts and **b** the time evolution of qualities for all roosts. Simulated bat population and social network dynamics with alternative roost dynamics in terms of **c** total number of bats, **d** number of connected components, **e** Morisita clustering index, and **f** degree centrality. Bat survival and recruitment are varied between simulations and error bars show one standard deviation over 5 replicate Monte Carlo simulations. All time steps are in years

To demonstrate dependence of the bat social network structure on the roost dynamics, we consider an alternative realization of the random roost generation and evolution process and corresponding bat population and roosting dynamics (Fig. 13.3). Computing the bat population and network observables as in the previous case, we again see a lack of correspondence between simulations when the time series of bat population is considered and a strong correlation between the Morisita index, degree centrality, and number of connected components. Due to the influx of new roosts at the beginning of the simulation that monotonically decrease over time in these alternative roost dynamics, we see the Morisita index and degree centrality in Figs. 13.3e and f increase with time for the same reason as in the last case: fewer roosts means bats must share roosts more, meaning clustering and communication degree are higher. In addition, the bat social network has more than one connected component at the beginning of the simulations, since the number of roosts is relatively large then; when the number of roosts decreases past a critical level, we see only a single connected component in almost every case.

13.6 Discussion

Our model provides a prospective method for developing hypotheses on aspects of habitat, population dynamics, and social ecology. Simulations using our model may best be thought of as exploratory, or null models. Indeed, comparing observed patterns of social structure under specific habitat characteristics to simulation results may be a useful way to identify individual parameters and mechanisms in need of study. For example, in our case study, we saw that (1) social structure was closely related to roost dynamics, but insensitive to bat population dynamics, and (2) loss of roosts resulted in highly clustered and centralized roost networks. Relative to our second result, in a field trial with the northern long-eared bat, Silvis et al. (2015) found that roost loss may actually begin fragmentation of bat colonies and their roost networks. Similarly, our model results suggest an inverse relationship between clustering and degree centralization and roost availability, but empirical field data suggest high centralization despite high roost availability (Ford et al. 2016). Why our theoretical results differ from field results may be an artifact of the simplified definition of each bat's roost selection probability distribution. Generally speaking, the differences between model and experimental results could indicate the presence of behavioral traits, such as signaling to conspecifics (Montero and Gillam 2015) that are inadequately understood across species, and highlights a potential area of inquiry.

Because relatively little is known about the relationship of bat social structure to roost dynamics, our model was created with incomplete data, and it therefore is unlikely that our model simulations will accurately describe social behavior in situ. Nonetheless, model output is informative for exploring the relationships among different behavioral and roost dynamics. In practice, it is difficult to know exact values for each of the free parameters. Although it is beyond the scope of our test case, it is possible to optimize model parameters to align simulation results and field results; doing so could be highly informative relative to uncovering true parameter values, and thus rules dictating bat behavior. More broadly, parameterizable agent-based models may be used to explore the interconnections among various aspects of bat ecology under scenarios that are not permissible in field settings (e.g., threatened and endangered species). Agent-based models also may be generalized and adapted to address additional topics such as disease dynamics and spatial factors. Although we did not incorporate these factors into our model, we note that incorporation of disease and spatial components is tractable, and we encourage others to consider these effects when using our model or developing additional models. Similarly, although we report only a small number of observables for our networks, it is trivial to calculate any network metric of interest.

13.7 Conclusion

Roosts long have been considered a critical component of bat habitat, and rightly so, given that roosts serve as nurseries, information centers, and protection from weather and predators. Consequently, protection of roosts and roosting areas has received considerable conservation focus. Despite the clear importance of roosts, and conservation efforts directed at protecting roosts, the impacts of roost loss on bats are poorly understood. Similarly, the mechanisms by which bats tolerate roost loss, and conversely, thresholds where tolerance is exceeded, are unknown. Limited understanding of the impacts of roost loss is particularly true at the group and social level, despite the fact that many benefits of social group membership are closely related to survival and recruitment. Two empirical field studies on very different species in substantially different habitats have shown that roost loss may alter social behavior, but with so few studies, it is impossible to generalize or draw conclusions. However, agent-based modeling offers a flexible and robust framework for simulation and prospective analysis that may be used to gain insight into impacts of roost loss on bats. We encourage both experimental studies on the impacts of roost loss on bat social groups and the use of agent-based models for these efforts.

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Chapter 14
The Influence of Sex and Reproductive Status on Foraging Behavior and Seed Dispersal by *Uroderma convexum* (Chiroptera: Phyllostomidae)

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Abstract *Uroderma convexum* construct and occupy tents. Tents serve as day shelters and reproductive sites, but also frequently are used as night feeding roosts. We observed and radio-tagged *U. convexum* occupying tents at Sarapiquí, Costa Rica. Social groups of *U. convexum* were composed of one adult male, reproductive females, and immature bats apparently forming a polygynous harem organization. We report spatial information (core-use, foraging range, habitat coverage use) and seed dispersal behavior for seven radio-tagged bats. Bats spend much of their foraging time in the riparian habitats; however, they also forage in mature and secondary forest and several anthropogenic habitats, dispersing at least eleven species

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of plants of different life forms. Bats establish night feeding roosts up to 1800 m from their day roost. Feeding roosts are in foliage close to plants producing ripe fruits and both feeding roosts and resource plants vary in space over time. Most of the time, adult males restrict movements to fruiting plants within 100 m of their tents and frequently return within the foraging period of the night, thus males disperse a large proportion of the seeds they handle exclusively within perturbed areas associated with the tents. In contrast to males, adult females usually do not return to a tent until near dawn and move over greater distances, frequently dispersing seeds into multiple habitats. Social organization, sex, and reproductive status appear to influence the outcomes of foraging behavior and seed dispersal of the bats.

14.1 Introduction

Many animals are noted for constructing shelters that offer protection from weather and predators, as well as places to rear offspring. These include numerous mammals that excavate burrows (e.g., rodents, moles, aardvarks, armadillos, carnivores, among others). Notable examples are the woodrats (*Neotoma* spp), round-tailed water rats (*Neofiber alleni*), muskrats (*Ondontra zibethica*), and beavers (*Castor fiber* and *C. canadensis*) for their behavior of introduction and inter-weave plant materials into house-like shelters above ground or under water. However, among more than 1300 recognized species of bats (N. Simmons *personal communication*), only a few invest time and energy to modify their environment for the purpose of creating a roost. *Lophostoma silvicolum* males are unique in carving holes with their teeth to modify termite nests which often continue to have living termites that actively aerate the nests (Dechmann et al. 2004); however, 22 species of bats are known to modify living plant parts, mostly leaves, in order to build "tents" for group shelters (Rodríguez-Herrera et al. 2007). Tent-making has evolved in the Pteropodidae in the genus *Cynopterus* which occurs in southern Asia and some Indo-Pacific Islands and in nine genera of the Phyllostomidae of the Neotropics.

Tent-making bats are social, they form groups. Group size in tents varies between seasons and species. The causes of sociality in tent-making bats remain unclear. Kerth (2008) suggests that ecological constraints such roost limitation, social thermoregulation, and longevity may promote sociality, but these constraints are not sufficient to explain the current frequency and diversity of group living in bats. Furthermore, it has been suggested that polygyny in tent-making bat species is based on the defense of the tent resource (Balasingh et al. 1995; Brooke 1990; Chaverri and Kunz 2006; Kunz and Lumsden 2003; Kunz and McCracken 1996; Kunz et al. 1994; Storz et al. 2001). The generally assumed hypothesis is that males make the tents and females select a male based on tent characteristics. Tent construction is also assumed to be a proxy for male display behavior in competition with other males for females (Balasingh et al. 1995; Kunz and Lumsden 2003; Kunz and McCracken 1996). Nevertheless, this hypothesis has never been tested and the little evidence available suggests that this assumption may vary according

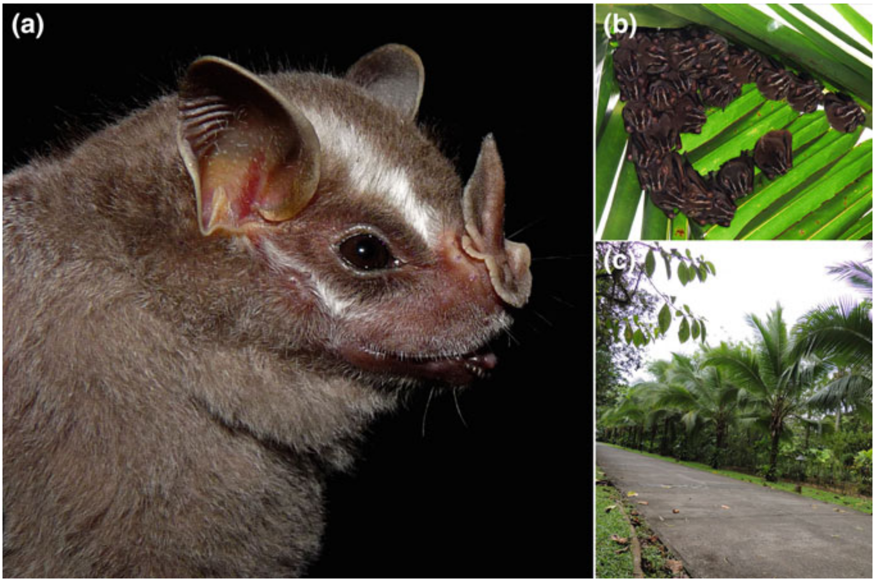


Fig. 14.1 **a** *Uroderma convexum*; **b** group of *U. convexum* in a pinnate tent, **c** coconut palms with tents of *U. convexum*

to species. For example, at least for the Honduran white bat, *Ectophylla alba*, not only the males construct their tents, females also contribute to this task (Rodríguez-Herrera et al. 2006, 2011). Unfortunately, the process of tent construction by Neotropical tent-making species had never been directly observed for most of the species, and until this information become available, assumptions have to be done regarding social life and implication of sex differentiation on the behavior of bats (e.g., foraging behavior) around their roosting resource.

Although tents are clearly important for day roosting, in this chapter, we focus primarily on the importance of this kind of roosts as central places for the nightly origin point for foraging movements in the phyllostomid *Uroderma convexum* (Fig. 14.1a). We discuss our findings in the context of the hypothesis proposed by Kunz and McCracken (1996) that adult males actively construct and defend tents in order to attract harems of breeding females while presenting spatial information on the size of foraging ranges and habitat use by adult males and adult females. We then present information on seed dispersal examining the relationships between tent locations, foraging areas, and the handling time associated with ingestion of fruits.

We tested the following predictions: (1) Given their tent defense behavior, nightly activity of adult males will be restricted to areas near roosting resources, which results in small movement areas; (2) Adult females will show less restricted movements during nightly activities, which results in larger movement areas than adult males; (3) If adult males do not restricted their movements close to tents, they probably will return frequently to their roosts during the night (monitoring pattern);

(4) Due to the reason that they are not constrained by tent defense, adult females may disperse seeds over greater distances and in more habitats than males.

14.1.1 Taxonomical, Behavioral, and Ecological Profile of *Uroderma convexum*

Mantilla-Meluck (2014) recognized five species of Uroderma throughout its geographic range (*bilobatum*, *convexum*, *davisi*, *magnirostrum*, and *bakeri* sp. nov.). Based on this work, *U. convexum* (Lyon 1902) is recognized as occurring from Ecuador, Colombia, and the Pacific coast of Panama west to Honduras and the Atlantic versant of Mexico. In Costa Rica, *U. convexum* typically inhabit lowlands of the Pacific and Caribbean coast, below 1200 m elevation (LaVal and Rodríguez-Herrera 2002; Rodríguez-Herrera and Wilson 1999). The diet of this genus is composed primarily of fruit with lesser amounts of pollen, nectar, and insects associated with fruits or flowers (Fleming et al. 1972; Gardner 1977; Handley et al. 1991). Uroderma as a genus consumes fruits of approximately 40 known plant species from 13 genera and 10 families (Lobova et al. 2009). *Ficus* species are prominent in the diet which also includes the genera *Piper*, *Philodendron*, *Cecropia*, *Solanum*, *Vismia*, *Quararibea*, *Clusia, Brosimum*, and *Psidium* (Gianini and Kalko 2004; Goodwin and Greenhall 1961; Lovoba et al. 2009). Its generalist frugivorous diet, habitat breadth, and abundance suggest that all five species of the genus are important seed dispersers of both small and large-seeded fruits promoting plant community diversity and secondary succession in open areas and forest fragments (Fleming 1988; Fleming and Heithaus 1981; Gorchov et al. 1993).

Uroderma roost by day under tents made from modified leaves of 18 identified species of plants (Figs. 14.1b and 14.2a, b; Barbour 1932; Kunz 1982; Rodríguez-Herrera et al. 2007). In many locations they prefer the pinnate leaves of *Cocos nucifera* for tent construction (Figs. 14.1b and 14.2a; Sagot et al. 2013;

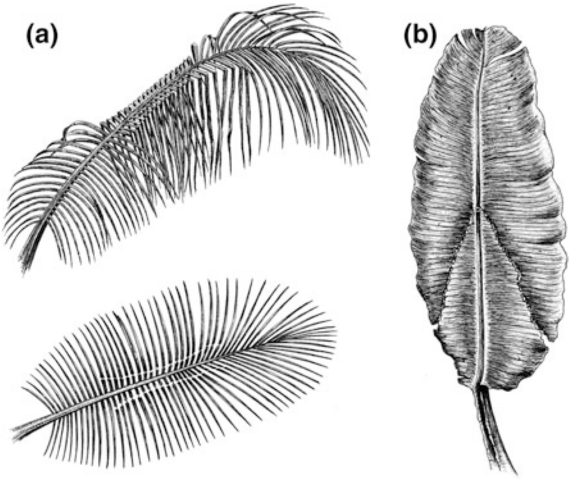


Fig. 14.2 Architecture of the tent roosts used by *U. convexum* at the study site. **a** Pinnate tents in *C. nucifera*; **b** paradox tent in *Musa* spp. Modified from Rodríguez-Herrera et al. (2007)

Timm and Lewis 1991). Occasionally, *U. convexum* roost in hollow logs, caves, unmodified leaves, and human buildings (Lewis 1992; Timm and Lewis 1991). The use of *C. nucifera* and other introduced plants have favored the presence of *U. convexum* tent roosts in anthropomorphic habitats such as plantations, gardens, and cattle ranches; however, this species also inhabits mature forest of various types (Bonaccorso 1979; Sagot et al. 2013).

Uroderma is gregarious (Fig. 14.1b), although usually found in groups of <15, it has been observed forming colonies with up to 59 individuals (Kunz 1982). Reproduction is a bimodal polyestry with immature flighted and independently foraging at about one month of age (Fleming et al. 1972). Social groups are composed of multiple females and dependent young with a single reproductive male present, suggesting a harem mating system (Baker and Clark 1987; Kunz and McCracken 1996).

14.2 Study Area

Our study was conducted between July 2012 and August 2013 at the Tirimbina Biological Reserve (TBR) and surrounding landholdings at La Virgen de Sarapiquí, Heredia Province, Costa Rica (Fig. 14.3). This area is tropical wet forest (Holdridge 1967) with elevation ranging from 40 to 150 m. Mean annual temperature is 25.3 °C and mean annual precipitation is 3900 mm (McDade et al. 1994). TBR includes primary, secondary, and riparian forest as well as a small abandoned cacao (*Theobroma cacao*) plantation. Surrounding landholdings form a matrix of anthropomorphic habitats including gardens, pastures, and diverse agricultural plantations.

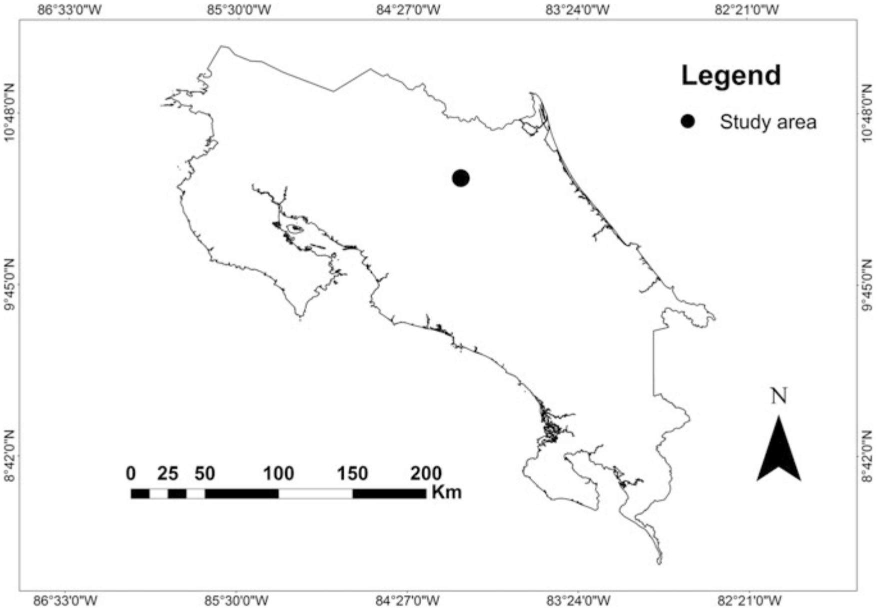


Fig. 14.3 Location of the study area. La Virgen de Sarapiquí, Heredia, Costa Rica

14.3 Methods

14.3.1 Capture of Bats

Our research protocols followed the guidelines of the American Society of Mammalogists (Sikes et al. 2011). Bats were captured under a series of modified pinnate tents made from coconut palm fronds and paradox tents made from banana leaves (Figs. 14.1c and 14.2b). Individual bats were captured during the day using a customized trap with an extendable pole designed to catch a group of bats within a tent. Bats also were captured at night using mist nets placed close to tents or fruiting trees. Upon capture bats were placed in soft cloth bags and taken to an enclosed area where they could be processed. Body mass and forearm length were measured using a 100 g Pesola spring balance (Baar, Switzerland) and CD-80C Mitutoyo digital calipers (Aurora, Illinois, USA), respectively. Individuals were classified as adult or immature based on the ossification of the epiphyseal growth plates of the phalanges (Anthony 1988). Reproductive status was determined from enlarged testes on males and pregnancy or lactation for females.

Captured bats were selected for two purposes: some were used for captive observations of fruit manipulation during feeding and others for radiotracking. Several individuals were used for both activities. Bats selected for radiotracking were fitted with a colored, split ring, plastic forearm band (Size X3, A. C. Hughes, Hampton Hill, United Kingdom) for long-term individual recognition and with a radio transmitter (model BD-2 N, Holohil Systems, Carp, Ontario, Canada). Transmitters were glued to the dorsal fur between the scapulae (Audet 1990; Bonaccorso et al. 2015; Waldien and Hayes 2001; Waters et al. 1999) using latex adhesive (Osto-Bond; Montreal Ostomy; Montreal, Canada). Transmitter mass was 0.5 g, < 3 % of body mass of the smallest bat that we radio-tracked. Bats were held in a soft cloth bag for 20 min to ensure that the adhesive securely bonded the transmitter to the fur. Bats were then released at the point of capture within 40 min of capture. Based on observations of tagged bat on their tents and recaptures of the animals, it appeared that transmitter's weight and plastic rings did not affect the bat's health or flight capacity.

14.3.2 Radiotracking

Bats were monitored during nightly tracking periods between 1730 and 0000 h. Multiple individuals were monitored in a given night using TRX-1000S tracking receivers and 3-element directional yagi antennas (Wildlife Materials, Murphysboro, Illinois, USA). Tracking stations were established within 10 m of tents and always <300 m from foraging areas for each bat. UTM coordinates of tracking stations, tents, night roosts, and fruiting trees were recorded using Garmin 12XL GPS units (Garmin Corporation, Olathe, Kansas). Azimuths from the tracking station to the bearing determined with the directional antenna were measured to the nearest degree using KB series sighted compasses (Suunto, Helsinki, Finland).

Observers frequently moved between tracking stations to improve radio signal strength and proximity to bat activity in order to reduce computational errors in determining bat positions. When radio contact with a focal animal was lost, we quickly re-established radio contact by walking in the direction of the disappearing radio signal. If two or more bats were within effective telemetry range, tracking data were taken every 3 min as possible rotating signal reception between multiple tagged bats. Flight and roosting were distinguished by a rapidly varying signal strength indicating flight and a steady signal at fixed directionality for at least 15 s indicating roosting (Bonaccorso et al. 2015; Rothenwöhrer et al. 2010). Each radio fix included records of time, signal strength from an analog meter, gain setting from gradations calibrated on the gain dial, the GPS position of the observer, and the activity of the bat (roosting or flying). Based on data inspection of the activity points and the capacity of bats of flying across the long axis of all measured foraging ranges in < 3 min, we concluded that all spatial points in our analyses were independent.

14.3.3 Calculation of Bat Locations

Telemetry locations for roosting bats were determined by homing (walking toward increased signal strength) to roosting bats or by triangulation using three or more positional fixes if roosts could not be approached because of physical barriers such as rivers or fences. Flight positions were determined from single azimuths along with distance, which was estimated from signal strength and gain following established methods of Bonaccorso et al. (2015), Law and Lean (1999), O'Donnell (2001) and Winkelmann et al. (2000). Approximate relationship of signal strength to distance (± 30 m error) was calibrated from transmitters set both at 2 and 15 m above ground at standardized gain settings along measured reception distances to 300 m. The majority of single bearing records were made with the observer <100 m from the transmitting bat while avoiding topographical features potentially causing severe refraction or reflection of radio signals.

Telemetry data at noted above including distance estimates between observer and bat were entered into Excel (Microsoft 2012). We used LOAS 4.0 (Ecological Software Solutions, Urnäsh, Switzerland) to plot triangulations of the estimated location of the bat; whereas, bat locations from single bearing telemetry were calculated using the following equations:

$$BN = (ON + D)\ \sin\Theta \tag{14.1}$$

$$BE = (OE + D)\ \sin\Theta \tag{14.2}$$

Where BN is the northing UTM location of the bat, ON is the northing UTM location of the observer, D is the estimated distance based on signal strength, Θ is the azimuth in radians from the observer to the bat, BE is the easting UTM location of the bat, and OE is the easting UTM location of the observer.

14.3.4 Landscape Spatial Analysis and Mapping

We employed a least squares cross validation to determine the smoothing parameter (Rodgers and Carr 1998) with minimum estimated error for fixed-kernel estimates (Seaman et al. 1999). From these data, we calculated minimum area probabilities for foraging range (FR) as the 95 % fixed kernels and Core-use Areas (CUA) as the 50 % fixed kernels. Kernel value calculations were obtained by Geospatial Modeling Environment (2009–12), ArcGIS (ESRI 2010) and (R Core Team 2013). Flight positions as well as night roosting positions were used to calculate FR and CUA. Long Axis across the foraging range (LAX) was determined by measuring the distance between the two farthest point locations within the FR. Finally, we calculated the percentage of activity of the bats within and beyond 100 m away from the day roosts (PAC).

To examine the use of the space by *U. convexum* and its potential relationship to seed dispersal, we transposed bat locations on a map of the study area using ArcGIS and classified the land cover as: (1) Forest: closed canopy upland forests; (2) Gardens: associated with horticulture; (3) Pasture: grasslands dedicated to cattle grazing; and (4) Riparian: bands of gallery forest along the Sarapiquí River and small streams. We tallied the number of telemetry positions for each bat that fell into each habitat category to obtain the percentage of use per habitat.

14.3.5 Seed Dispersal

In addition to the use of tents by *U. convexum* as day shelters (Barbour 1932; Kunz 1982; Rodríguez-Herrera et al. 2007), tents also are used for feeding at night (Rodríguez-Herrera et al. 2007). We noted the number and species of seeds discarded under tents by *U. convexum* following the sampling methods used by Melo et al. (2009). We searched for and sampled pinnate tents in *C. nucifera*, due to the high density of these tents in gardens and along roads of Sarapiquí (Sagot et al. 2013). Tents with *Uroderma* are occasionally found in closed canopy forest; however, because other bat species may use these tents in this habitat, we excluded such tents from our seed analysis (Rodríguez-Herrera et al. 2007). Pinnate tents of *C. nucifera* in the study area were scanned for seeds on the soil surface in 1 m^2 quadrats immediately beneath tents. We also collected seeds in control quadrats established in each of the four cardinal directions 5 m away from each tent. We differentiated between bat-generated and non-bat seed rain by characteristic tooth and claw marks of the bats. All seed collection was restricted to seeds >8 mm length (large seeds) because smaller seeds are difficult to identify and may be carried away by water run-off or ants (Melo et al. 2009). Buried seeds were excluded to avoid older seed rain that may have occurred before tent construction. We excluded those seed species found in similar densities in both tent and control quadrats. Seeds collected were identified to the finest taxonomic level and classified according to associated habitat (Table 14.3). We also examined the diets of our radio-tagged bats based upon visual inspection of fruiting trees having ripe fruit crops in areas frequently visited by tagged bats or from fruits found under feeding roosts.

14.3.6 Captive Observations of Fruit Manipulation by U. convexum

We employed a screened tent to observe fruit manipulation and consumption by bats. We offered one male and one female in each trial fresh ripe fruits, either *Ficus insipida* or *F. citrifolia,* obtained each day from fruiting trees in the area. Fruit height and width were measured with CD-80C Mitutoyo digital calipers (Aurora, Illinois, USA), weighed with a ACP-200 Digital pocket scale (American Weigh Scales—Georgia, USA), and numerically marked with ink. Fruits were offered to the bats attached by paper clips onto a horizontal rope 2 m above the ground. For each feeding attempt, we noted the identity of the bat, time taken consuming the fruit and the fruit mass consumed (difference between the initial wet mass of the entire fruit and the mass of discarded fragments). We used a Sony DCR-SR45 digital video camera recorder with night vision (Sony, New York, USA) to recorded and analyzed fruit consumption behavior. We only included in our analysis for fruit handling time fruits that were entirely consumed.

14.3.7 Statistical Analysis

We compared FR, CUA, PAC, and habitat use among sexes using one-way ANOVAs with an a posteriori test of Tukey's Honest Significant Difference (Tukey HSD). Also, 2-way ANOVAs were performed to compare fruit consumption time and initial fruit wet mass among sexes. For the analyses of PAC, processing time of fruits of *F. citrifolia* and habitat use (from gardens only), we employed a logarithmical transformation to fit the parametric analyses. We used a Kruskal–Wallis rank sum test for comparison of LAX between sexes. Although we radio-tagged and tracked 10 bats, we excluded from our spatial analyses of FR, CUA, and LAX all immature bats and individuals that had ≤100 total telemetry location points. All numerical results reported in the text are means and standard errors. All analyses were conducted using (R Core Team 2013) with an alpha level of ≤0.05.

14.4 Results

Seven *U. convexum,* represented by three adult males and four adult females were radio-tracked for two to ten calendar days (4.71 ± 1.06 days/bat). We collected a total of 1236 telemetry locations for these seven individuals (Table 14.1). Sub-adult

Table 14.1 FR, CUA, and LAX of *U. convexum* at Sarapiquí

Sex/ind.	Month/year	Tracking nights	Telemetry positions	95 % FR	50 % CUA	LAX	Activity ≤100 m from tent
		(n)	(n)	(ha)	(ha)	(m)	(%)
M2	Jul-12	10	423	7.7	1.1	1817	94.5
M3	Aug-13	2	103	20.1	4.9	583	26.2
M4	Aug-13	3	111	20.2	4.0	601	18.0
F3	Jul-12	7	144	23.2	3.7	872	8.3
F4	Aug-13	3	160	28.7	4.2	848	3.1
F5	Aug-13	4	170	39.5	7.9	1135	8.8
F6	Aug-13	4	125	26.1	3.7	783	17.6
Mean ± SE		4.71 ± 1.06	176.57 ± 42.11	23.63 ± 3.66	4.21 ± 0.76	948 ± 160.9	25.21 ± 11.90

M Adult male; *F* Adult female

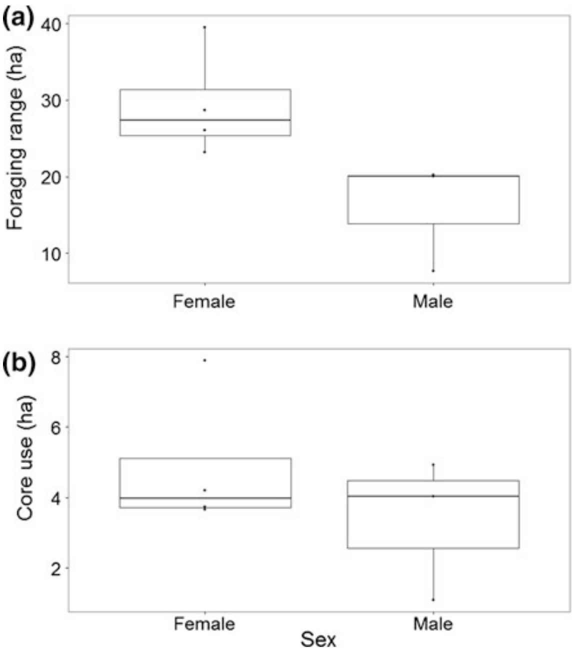


Fig. 14.4 Median (quartiles and range) of the FR (**a**) and CUA (**b**) of male and female *U. convexum* at Sarapiquí

male M1 and adult females F1 and F2 were excluded from our analysis of FR, CUA, LAX, PAC, and habitat use because of small sample sizes <50.

Mean FR for *U. convexum* was 23.6 ± 3.6 ha (*n* = 7 bats; Table 14.1). Although a one-way ANOVA slightly missed significant difference between female and male FR (Tukey HSD test, *P* = 0.06) in part due to high variance, females trended toward higher median values of FR than males (Figs. 14.4a and 14.5a).

Mean CUA was 4.21 ± 0.76 ha (*n* = 7 bats; Table 14.1). There were no significant differences between sexes in CUA (TukeyHSD test, *P* = 0.37). Females and males had similar CUA medians; however, again there was high variation in individual values for both sexes (Figs. 14.4b and 14.5b).

Mean LAX was 948 ± 161 m (*n* = 7 bats; Table 14.1). There were no significant differences between sexes in LAX (Kruskal-Wallis chi-squared, *P* = 0.48). Adult females had median values of LAX larger than adult males (Fig. 14.6a). Nevertheless, males had highly variable movements and sometimes moved long distances from their tents (e.g., bat M2 in Table 14.1).

The mean PAC within 100 m from tents was 25.2 ± 11.9 m (*n* = 7 bats; Table 14.1). For adult males, 46.2 ± 24.2 % of all total activity locations from telemetry were within 100 m of their tents, while for adult females this represented only 9.4 ± 3.0 % of all activity points (Fig. 14.6b). There was a significant difference between the percentages of activity as a function of distance from tents between sexes with males active closer to tents (TukeyHSD test, *P* = 0.05).

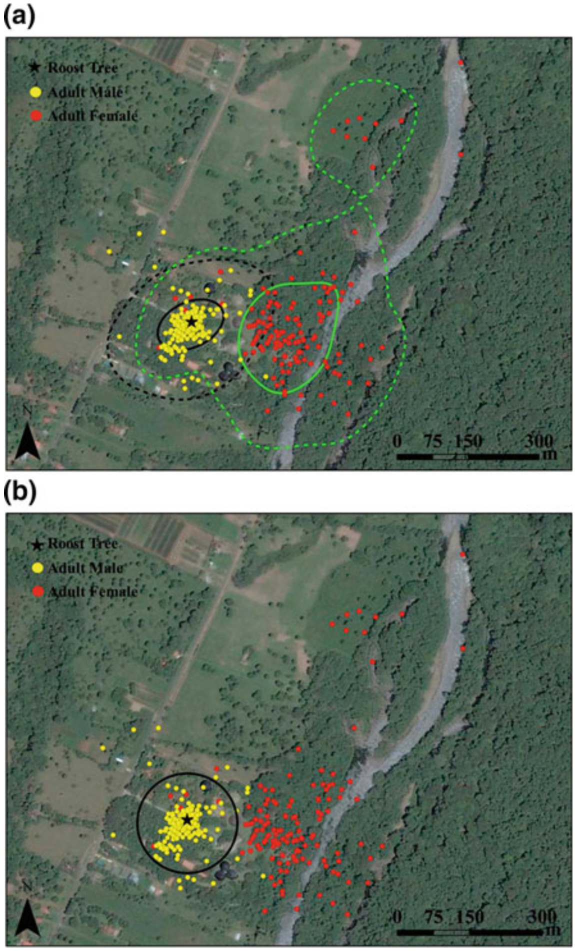


Fig. 14.5 **a** 95 % FR kernels (dotted lines) and 50 % CUA kernels (solid lines) of two representative bats occupying the same tent, male 2 and female 4. **b** Scatter plot of FR of male 2 and female 4 depicting the strong tendency to remain close to the tent by this male. The circle around the tent location is a 100 m radius

Uroderma foraged in a variety of habitats as follows (Table 14.2): riparian (42.7 ± 9.9 % of all telemetry positions), gardens (31.3 ± 11.6 %), closed canopy upland forests (21.9 ± 5.4), and pastures (4.1 ± 0.9 %). Females showed significantly higher percentage of activity (61.7 ± 4.9 % of total locations) than males (17.4 ± 8.7 % of total locations) in riparian forest (one-way ANOVA TukeyHSD test, $P = 0.005$ and Fig. 14.7). The use of gardens also differed significantly between sexes (TukeyHSD test, $P = 0.01$; Fig. 14.7). Adult males used gardens (54.8 ± 21.2 % of total locations) more than females (13.7 ± 1.5 %). There was no significant difference between females and males in the use of closed canopy upland forests (TukeyHSD test, $P = 0.69$) or pastures (TukeyHSD test, $P = 0.41$).

Four adult males and three adult females were used during captive observation of fruit manipulation. We recorded 12 feeding observations for *F. insipida* (males = 5 and females = 7) and 21 feeding observations for *F. citrifolia*

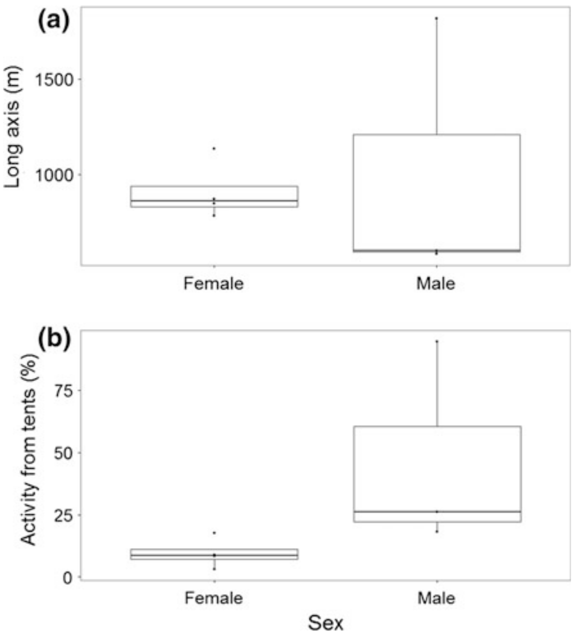


Fig. 14.6 Median (quartiles and range) of the LAX (**a**) and the percentage of activity ≤100 m from tents (**b**) for male and female *U. convexum* at Sarapiquí

Table 14.2 Habitat use of *U. convexum* at Sarapiquí

Bat I.D.	Telemetry positions (n)	% of Telemetry positions by habitat			
		Riparian	Forest	Pasture	Garden
M2	423	0.5	0.5	1.9	97.1
M3	103	29.1	35.9	1.0	34.0
M4	111	22.5	37.9	6.3	33.3
F3	144	54.9	27.1	3.4	14.6
F4	160	60.6	18.8	4.3	16.3
F5	170	55.3	27.1	8.2	9.4
F6	125	76.0	6.4	3.2	14.4
Mean ± SE	176.6 ± 42.1	42.7 ± 9.9	21.9 ± 5.4	4.06 ± 0.9	31.3 ± 11.5

(males = 2 and females = 19). Bats usually consumed more than 50 % of the wet mass of all figs before discarding them (51.6 ± 2.6 for *F. insipida* and 57.5 ± 3.6 for *F. citrifolia*). However, entire *F. insipida* were consumed in 43.5 ± 3.7 min (n = 12), in contrast to 4.8 ± 0.2 min for *F. citrifolia* (n = 21) (Fig. 14.8a, b).

Statistical analyses (2-way ANOVAs) indicated no significant differences in processing time of *F. insipida* (F = 0.501, $P \geq 0.49$; Fig. 14.8a) or *F. citrifolia* (F = 0.964, $P \geq 0.34$; Fig. 14.8b) among sexes. No significant differences were found neither in the interaction between sex and wet fruit mass for *F. insipida* (F = 0.065, $P = 0.81$) or for *F. citrifolia* (F = 0.366, $P = 0.55$).

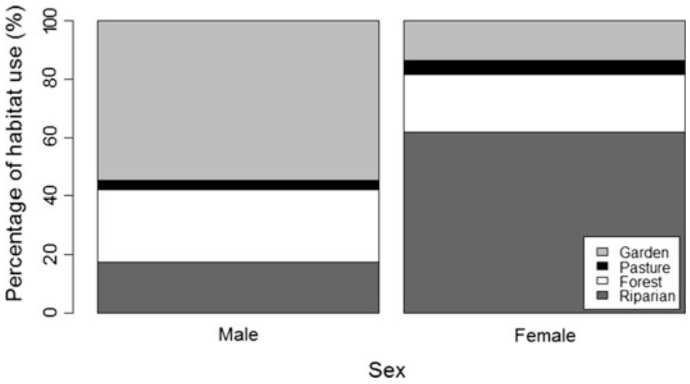
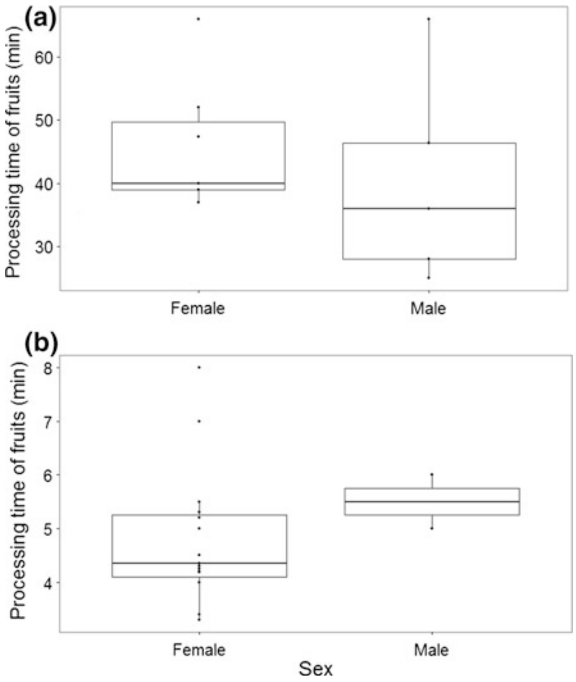


Fig. 14.7 Percent habitat use for adult males and female *U. convexum* at Sarapiquí

Fig. 14.8 Median (quartiles and range) of the consumption time of ripe fruits of *F. insipida* (**a**) and *F. citrifolia* (**b**) by *U. convexum* at Sarapiquí



We found 321 large seeds representing 6 plant species in our quadrats that showed signs of manipulation by bats (e.g, tooth marks and removal of pulp/arils) (Table 14.3). All large seeds dispersed by *U. convexum* represented either dicot or monocot tree species including palms and were associated with different forest successional stages (Table 14.3). *Spondias radlkoferi* (*n* = 154, 48.0 %) and *Calophyllum brasiliense* (*n* = 148, 46.1 %) accounted for most of the large seeds in

Table 14.3 List of plant species in the diet of *U. convexum* at Sarapiquí from seeds found under tents and plants visited by radiotagged bats

Family	Species	Detection*	Number of seeds	Associated habitat (s)	Life form
Anacardiaceae	*Spondias radlkoferi*	FR	154	Mature and secondary forest	Tree
Calophyllaceae	*Calophyllum brasiliense*	FR	148	Mature forest	Tree
Sapotaceae	*Pouteria* sp	FR	12	Mature forest	Tree
Humiricaceae	*Sacoglotys trichogyna*	FR	4	Mature forest	Tree
Arecaceae	*Astrocaryum alatum*	FR	2	Mature forest	Palm
Simaroubaceae	*Simarouba glauca*	FR	1	Mature and secondary forest	Tree
Moraceae	*Ficus insipida*	T	–	Mature and secondary forest	Tree
Moraceae	*Ficus citrifolia*	T	–	Mature and secondary forest	Tree
Moraceae	*Ficus popenoei*	T	–	Mature and secondary forest	Tree
Cecropiaceae	*Cecropia* sp	FR	–	Secondary forest	Tree
Solanaceae	*Solanum* sp	FR	–	Secondary forest	Shrub

**FR* Feeding roost; *T* Feeding tree

quadrats under tents (Table 14.3). All remaining seed species represented ≤4 % of total seeds. We qualitatively documented small-seeded plants in the diet of *U. convexum* both during visual inspections in the activity areas of radio-tagged bats and from seeds dropped by bats in quadrats placed under tents.

14.5 Discussion

Males of several tropical bat species are demonstrated to fight for dominance to secure access to females, either directly by defending groups of females or indirectly by monopolizing resources (Kerth 2008). For example, in both *A. jamaicensis* and *Saccopterix bilineata*, dominant males attack male intruders resulting in higher paternity success for these males within their own harem than do subordinate males which sometimes are tolerated in the harem, or satellite males which form separate roosting groups (Nagy et al. 2007; Ortega et al. 2003). In this context, our result indirectly support the hypothesis of male tent defense proposed by Kunz and McCracken (1996), and at least for the tent-making bat species *U. convexum*, we were able to confirm all of our predictions. It seems like the differences found between male and female behavior in FR, PAC and habitat use were influenced by the harem social system present in this species.

Our first and second prediction was supported by the differences in the foraging range and percentage of activity within and beyond 100 m away from the day roosts calculated for both sexes; with females showing larger foraging areas than males and significantly more activity away from the imaginary 100 m radius circle around tents during nightly foraging periods. In contrast, tent occupying males, when possible often would forage primarily on fruiting trees within 100 m of the tent. Much of the activity of the adult males was associated with anthropogenic gardens where tents in *C. nucifera* and *Musa* spp. usually are located. Our field observations and radiotracking data confirmed that adult males of *U. convexum* often carried fruit back to the tent or a foliage perch within view of their tent, contrasting to the behavior of adult females that generally only return to tents after foraging is concluded each night. With respect to our third prediction, we identified that although the general pattern of adult males was to restrict their movements close to their roosts, spatio-temporal changes in the availability of food resources can influence the movements of bats, potentially forcing the individuals to fly larger distances in order to get food, consequently increasing the size of their foraging range. This situation was confirmed with our tagged bats M3 and M4, which showed larger foraging ranges and less percentage of activity close to the tents than individual M2. Despite this, these individuals were more restricted to their roosts than all females monitored, in addition that we were able to confirm that they usually return during the night to the roosting area, probably in order to monitoring their roosts.

Regardless of the size of foraging range, monthly activity of *U. convexum* was concentrated in very small core-use areas, which change as fruiting trees sequentially produce ripe crops (Table 14.1). These small areas reflected the abundance, nutritional quality (especially high in calcium), and asynchronous fruiting of fig trees throughout the year in tropical forests (Bonaccorso 1979; Shanahan et al. 2001).

Regarding the role of bats as seed disperser, it seems that *U. convexum* is a habitat generalist and individuals frequently moved through several habitats within a night while foraging (Fig. 14.7, Table 14.2). At Sarapiquí, these bats used all four of the major habitat classes defined by us from land cover maps and moved between several feeding trees, from fruiting trees to night feeding roosts, and to and from its tent in the course of a night, effectively transported seeds well beyond the canopy of parent trees. Seed dispersal by *U. convexum* included many disturbed and mature natural habitats. Bats dispersed both small-seeded species while flying and deposited under feeding roosts and tents, as well as large-seeded plants deposited almost exclusively under roosts and tents (Rodríguez-Herrera et al. 2007).

At more specific level, it seems that sex differentiation influences the outcomes of the seed dispersal process carried out by *U. convexum*, partially confirming our fourth prediction. Both sexes used the four categories of habitat, consequently dispersing seeds in all these areas, nevertheless the percentage of activity differed between males and females, especially for those habitats classified as riparian and gardens (Fig. 14.7). Riparian habitats were used more than any other habitat by females and include many fruiting trees found in the diet of *U. convexum*. Direct observations confirmed frequent riparian habitat visitation of adult females F3 and F6 at *F. insipida* and *F. popenoei* having ripe figs.

The probability of finding *U. convexum* presence is highly associated with microhabitat variables, and with the presence of coconut palms (Sagot et al. 2013). In fact, all of the tents occupied by tagged individuals were located in gardens, and many of the native fruiting trees included in the diet of this bat species (Table 14.3) also can be found in this habitat. For example, one *F. citrifolia* tree frequently visited by bats M1, M2 and F2 was located in a garden < 10–20 m from several tents. The abundance of coconut palms and bananas commonly used to construct tents combined with the food resources probably influenced the high amount of activity of *U. convexum* in this anthropogenic environment. Higher levels of activity of adult males on this habitat (Fig. 14.7) were expected due to the tent defense behavior that restricted the movements of individuals to areas close to their roosts.

In the case of pastures and canopy upland forest, there were no evident differences between the percentages of activity of both sexes. Pasture was the habitat least visited by *U. convexum* and was mostly used for transit between other habitats. However, bats occasionally visited remnant fruiting trees in this habitat for feeding. Because phyllostomid bats create a seed rain, particularly of small-seeded species (e.g., *Ficus* spp., *Cecropia* spp., *Solanum* spp.) by defecating while flying (Arteaga et al. 2006) they assist the regeneration of abandoned pasture with seed rain from forests. On the other hand, high densities of food availability in the upland closed canopy forests is expected to be one of the most important variables influencing the movements of individuals within this habitat, especially considering that some plant species found in the diet of *U. convexum* are typical of mature forests (Table 14.3). Phyllostomid bats facilitate the reproductive success of plants in both highly disturbed areas and closed forest habitats, favor the maintenance of plant diversity, and make possible the dispersion of plant species across landscapes both through seed (and pollen) translocation (Ávila-Cabadilla et al. 2014; Vleut et al. 2013).

Finally, observations of fruit manipulation showed that captive *U. convexum* handling time for consumption of fruits was highly dependent of fig size and that there was no difference among sexes. Time invested by *U. convexum* in handling large fruits (i.e., *F. insipida*) was higher than time invested in small fruits (i.e., *F. citrifolia*). Independent of the time invested in feeding on a fruit, *U. convexum* frequently consumed a high percentage of total fruit mass ($\geq 50\ \%$) for both *F. insipida* and *F. citrifolia*. Heer et al. (2010) demonstrated that *Artibeus jamaicensis* positively influences the germination success of the fig seeds ingested by removing pulp from around seeds in the digestion process. The consumption of fig fruits by *U. convexum* likely also helps *F. insipida* and *F. citrifolia* seeds to have enhanced germination success. Fruits with small seeds generally contain large numbers of seeds (e.g., *F. citrifolia* have a mean of 274 ± 13.9 seeds per ripe syconium; range = 202–314; $n = 8$). Considering that *U. convexum* was able to eat an entire ripe *F. citrifolia* fig in 4.8 ± 0.3 min, one bat potentially will disperse several thousand small seeds in multiple habitats within their foraging areas each night.

Our results demonstrated that, independent of the sex, *U. convexum* constantly move seeds from trees located in both mature and successional upland and riparian forests to highly disturbed areas such as gardens, pastures, and other agricultural landscapes. Large movements (LAX) of some individuals (i.e., 1817 m), in addition that some of our radio-tagged bats (F1 and F2) moved even farther when radio contact was lost no doubt facilitate long-distance dispersal, especially for small-seeded plant species. In contrast, loyalty to a few specific feeding roosts probably reduces the efficiency of the dispersal performed by *U. convexum* on large-seeded plants considering that the localities where the seeds are dropped are few. Nevertheless, survival rates of the seeds under these bat roosts are not documented as yet, and based on field observations, there are some level of seed germination under tents and feeding roosts in disturbed habitats, which results in the positive establishment of seedlings of some plants such *Cecropia* spp, *C. brasiliense,* and *S. radlkoferi*.

In conclusion, our study is the first in analyze the nightly behavior of a Neotropical tent-making bat species in the context of the hypothesis proposed by Kunz and McCracken (1996). Although we were not be able to document tent construction by males of *U. convexum*, our data suggests that activity patterns of adult males seems to respond to the defense of roosting resources. Differences in activity patterns of both sexes also influenced the role of bats as seed dispersers. Larger range of movements and the plasticity in habitat use of adult females will result in differences in the distance of the seed dispersal (females moved greater distances) and in the proportion of time expended in the habitats where the seeds will be deposited. Social behavior of *U. convexum* in conjunction with the quality of seed dispersal bears interesting potential for further testing among the variety of tent-constructing bats in Central America.

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