

# 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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J.W. Bradbury (✉)

Department of Neurobiology and Behavior, Cornell University, Ithaca, NY 14853, USA  
e-mail: jwb25@cornell.edu

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, *Vampyrus 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 epomorphine 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 pot-hole 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 demographics 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 pre-occupation 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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