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In memory of
Henry Lewis Adams III and Josephine Vince Adams,
the best parents a boy could have

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Introduction

A twitch, a twitter, an elastic shudder in flight
And serrated wings against the sky
Like a glove, black glove thrown up in the light
And falling back.

—D. H. LAWRENCE, "BAT"

Few poets have portrayed bats as elegantly as D. H. Lawrence, for their unique and fascinating nature makes them difficult to describe in words. Often, our contact with bats happens in fleeting and erratic glimpses that provoke deeply held fears and irrational reactions. Beyond reality, they are sometimes perceived as spawns of Satan, raising havoc; in their wake, disease and destruction follow. Even for the rationally minded, these winged night shadows dance at the edge of reality, confusing our senses and appearing unnatural, but natural they are. Evolution's tinkering is adventitious and in the case of bats undauntedly adventurous in bringing to life the only true flying mammal. Aloft on the winds of deep time, Lawrence's "black glove thrown up in the light" eventually encircled the globe, alighting on all continents except Antarctica. Indeed, from the original "glove," many forms blossomed through the eons and, in time, into human consciousness. Indeed, our species' common use of caves and cliffs over the last 300,000 years certainly entailed routine and lucid interplay with bats. Ultimately, however,

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our prolific imagination twisted them into the supernatural and mythical creatures that pervade historical and contemporary literature today.

Even after centuries of scientific study, bats remain amorphous specters or imaginary creatures to many. Perhaps, in some way, their lasting mythos is testimony to their magnificence. Having the capacities to effortlessly navigate darkness by vocalizing sounds we cannot hear while moving rapidly on stunningly acrobatic wings, they are undeniably unique to encounter. Even bat biologists who have dedicated decades to forming close and profound relationships with bats never become desensitized to their inimitable abilities and inherent vitality.

For those not professionally dedicated, developing an appreciation for bats may require some initial vocation to the task. However, through education, irrational fears are being replaced with a factual accounting of and even admiration for the truly wonderful world of bats. Many have unexpectedly found that the real-life story of bats is more astounding and interesting than fabled tales of the crypt and the macabre. This psychological ignition point has immensely helped dispel many of the age-old, contemptuous attitudes toward bats, and their lives have undoubtedly improved because of those efforts. But challenges remain as populations continue to decline globally.

In the twenty years since the first edition of *Bats of the Rocky Mountain West* was published, a tremendous amount of knowledge has been garnered, which certainly inspired this second edition. With advances in research technology, biologists are able to learn more about the secretive lives of bats; as a result, many of our preconceived notions about them have proven incorrect. Bats, as it turns out, harbor few diseases contractible by humans and, as mammals go, are exceptionally clean. Despite their generally small body size, some bats may live forty+ years, most species give birth to only a single young per year, maternal care of the young is altogether indulgent, and they are now known to have socio-emotional lives equivalent to those of dolphins, whales, elephants, and higher primates, including apes. Furthermore, bats are important to many ecosystems, devouring many tons of insects and saving our agricultural industry billions of dollars annually. They are also primary pollinators for important North American plants such as saguaro and organ pipe cacti and are long-distance dispersers of the seeds for many tropical plants, including those most important in forest regeneration. Comprising about 23 percent of all living mammalian species, they are one of the most successful groups on Earth, yet many species are critically endangered.

Although this book is about the bats of the Rocky Mountain West, more broadly, it is an invitation to better appreciate bats, not as mythical creatures but as intriguingly beautiful animals that represent part of our diverse world. Like ripples across a pond, I hope readers of this book will "pass the word" about the beauty of bats, thereby furthering public education, understanding, and appreciation of how they—mostly under the veil of darkness—profoundly and positively influence our lives. Although unseating people's misconceptions and irrational fears remains challenging, I hope this book is a welcome contribution to this effort and will effect change for years to come.

The intended audience is both the layperson and the wildlife specialist. The scope of this book includes bats found in the Rocky Mountain West states of Montana, Idaho, Wyoming, Colorado, New Mexico, and Utah, as well as Arizona, which is linked geologically and ecologically to the Southern Rockies by the Colorado Plateau. I begin here with a general discussion of the biology of bats, followed by a description in chapter 2 of the variable and complex landscapes of the region and how bats fit into them. In chapter 3 I discuss the evolution of bats as related to the Rocky Mountain West, whereas chapter 4 covers bat populations and community trends, feeding strategies, and resource use. Chapter 5 explores the strategies, achievements, and future goals for the conservation of bats in the region.

A key to species begins the section on species accounts that provide a picture and distribution map for each of the thirty-two species covered. The accounts are intended for use by specialists and laypersons alike. For the layperson, information on the natural history of each species is presented, whereas the specialist will find technical information on standard measurements, dental formulas, and subspecies distributions. In addition, sections on ecology/behavior and reproduction/development, as well as conservation status and threats, are presented based on peer-reviewed, primary literature for the region. A glossary of terms is provided at the back of the book.

Appendix 1 provides total numbers of threatened bat species by risk category from the International Union for the Conservation of Nature (IUCN) for 2003, when the first edition of *Bats of the Rocky Mountain West* was published, and 2023 (see table A1.1), as well as short descriptions of worldwide government agencies and nongovernment conservation groups and recognizes their efforts in the areas of bat monitoring and conservation. My hope is that readers will use these as convenient references to stimulate their involvement with organizations that promote the conservation of and educational outreach about bats. Appendix 2 offers a bibliography of government agency reports and documents, many of which, like bats, rarely see the light of day. I hope this is helpful in disseminating useful information to wildlife enthusiasts and academic biologists alike.

What's New in the Second Edition?

The second edition is heavily edited and updated to include the current state of knowledge on bats at its writing. Indeed, over the last twenty years, we have learned much more about bats that continues to amaze scientists. The thirty-two species accounts presented herein have been updated taxonomically with information on distribution, ecology, sociality, reproduction, and behaviors that paint a much fuller picture of Rocky Mountain West bats. In addition, new illustrations are provided throughout, as are amazing new photographs of bat species provided by Dr. Merlin Tuttle of Merlin Tuttle's Bat Conservation (www.merlintuttle.org), who has been photographing bats around the world for more than forty years. The literature section and the key to species have also been updated and refined. Species accounts are updated in terms of distribution maps, and full-spectrum spectrograms of representative sonar calls for most species are provided.

New sections have been added involving topics unknown or little known at the time of the first edition. For example, recent studies have shown that bats' elaborate social lives are equivalent to what we have discovered in other cognitively profound organisms such as monkeys, apes, humans, dolphins, whales, and corvid birds like crows and ravens, forming multilevel friendships that last decades. Unfortunately, also over the last twenty years, threats to bats have increased significantly due to human-induced climate warming, large-scale installations of wind farms, and overt habitat destruction and alterations. Humans' unwitting introduction of a European fungus into North American caves has killed millions of bats in the last seventeen years. In addition, the blaming of bats for various human-infecting viruses has caused fear and actions against bats on a global scale not previously seen. As we traverse the first quarter of the twenty-first century, our knowledge of bats has grown considerably. Although we have just scratched the surface of batness, one thing that is abundantly clear is their importance to the health and stability of nearly every ecosystem. Equally clear is the decline in bat numbers worldwide. In fact, on many continents, including North America, some species may become extinct before much, if any, of their natural history is even documented. Between 2020 and 2023, more than 100 bat biologists evaluated the status of North American bat species and found that 52 percent of the 154 species are at risk of declining precipitously in the next fifteen years due to human degradation of habitats and human-induced climate change.

From Aristotle to Cuvier to Now: Deciphering the Reality of Bats

Bat biologist Donald R. Griffin (1958) once stated: "Bats are such unusual creatures that some effort is required to think of them as actual animals living in a world of common sense and concrete reality." Bats are indeed mysterious to humans. Cloaked by the darkness of night, they remain elusive to our senses and challenging to decipher.

Scientific inquiry about bats dates back to antiquity. Nearly 2,500 years ago, Aristotle formally described the anatomy of bats, and in 1693 John Ray first categorized them as mammals instead of birds, although he did remain confused about their wings. Carl Linnaeus, who in 1758 began the formal science of taxonomic classification with the publication of his book *Systema Naturae*, assigned the then known seven species of bats to the order Primates, along with humans, all other known monkeys, apes, and colugos (flying lemurs). In the mid-1800s anatomists E. Geoffroy Saint-Hilaire and Georges Cuvier proposed a new order for bats called Chiroptera (whose name is taken from a Greek term meaning "hand-wing"). For the first time, the taxonomic relationship that isolated bats from all other mammalian orders was established. However, the science of taxonomy and systematics does not typically disseminate its findings to the public at large, so misconceptions remained—such as bats are flying mice—and these misconceptions occur across many cultures and languages. Professor David Armstrong writes about the linguistic juggling of the various words used for bats, uncovering the underlying conceptual miscues in the process:

> The German word for "bat," *Fledermaus*, means "flying mouse," as does the Russian *lyetuchya meesh*. Although certainly the reference to flight is correct, bats are not at all closely related to rodents. In English, bats were referred to as *nattabatta*, "night bat," perhaps of Scandinavian origin. *Aftenbakke* ("evening bat") is Danish for bat, and reference is made using *nattbacka* ("night bat") in Swedish. Possibly, all of these names are traceable to the poetic Icelandic word for bat, *ledurblaka*, meaning literally "leather flutterer." The Italian *pipistrello* (hence the genus *Pipistrellus*)

> apparently evolved from the Latin *vespertilio*, perhaps from *vesper*, "evening," plus *papilio*, a curious word meaning both "moth" and "the soul of the dead." French gets it all wrong; *chauve souris* translates to "bald mouse," mostly untrue, even for the most senior of individuals. Spanish miscues with *murcielago*, a corruption of *murciegalo*, "blind mouse," neither of which is true of bats. (Armstrong 1995: 1)

Unfortunately, even today, many people still think bats are related to rodents such as mice or rats; in reality, bats are no more closely related to those groups than are humans. We know from several hundred years of anatomical study—especially on teeth and, more recently, using molecular techniques—that the living group most closely related to bats capable of laryngeal echolocation is the order Soricomorpha, which includes shrews and moles. However, a large group of bats in a single family, the Pteropodidae within the order Chiroptera, does not, and apparently never has, been able to produce ultrasonic echolocation, making their relationship to the other twenty families of bats questionable.

The Precise Origin of "Batness" Still Evades Us

The farther back we peer into the ancient history of life on Earth, the less familiar life appears. To see the origin of bats, we need to squint backward at least 55 million years and probably much farther to uncover what we might call the ancestral "protobat" to today's denizens. Thus far, the fossil record has revealed no truly intermediate specimen between partially and fully formed bats. Thus, we are mostly left with conducting morphological and molecular analyses of contemporary species for traits and genes that have persisted across the ages and therefore may give some insights into the terrestrial or arboreal ancestor of bats. However, in reality, such an approach is akin to using the most advanced jetliners to find remnant clues of the Wright brothers' *Kitty Hawk Flyer* or perhaps even Henri Giffard's steam-engine–mounted dirigible flown in 1852, fifty years before the *Kitty Hawk Flyer*. Even though these early flying machines are dramatically different from today's versions, they had to be "adapted" to operate on the ground as well as in the air. Therefore, certain elements of design are consistent across time and have been carried forward, creating a certain level of continuity in disparately related flying machine lineages. From a biological standpoint, we see similar, but more deeply ingrained, continuity in that present-day anatomical structures (and we assume behaviors) are elaborations of more ancestral forms, not forged de novo as an engineer might bring about mechanistically. For example, understanding the evolution of horses using the fossil record requires looking for traits still possessed by present-day horses that were evident in extinct ancestors. Indeed, today's horses possess skeletal traits that first evolved nearly 34 MYA in the "dawn" horse (*Hyracotherium*) fossils, even though it was only the size of a house cat. We can then surmise the probable ancestral lineage leading to this early "protohorse" by extending its unique character stages to even earlier fossils. But can this work for bats when they had to forsake many of the characters that evolved from moving on the ground or climbing trees into those adaptive for flight?

Broadening our view, perhaps birds—the only other present-day vertebrate capable of powered flight—can provide a helpful model for pursuing this dilemma in bats. Although the ancestral beginning of birds can be clearly traced to a lineage of therapod dinosaurs that were terrestrially bipedal and possessed feathers evolved for thermoregulation, how and why did this lineage take to the air? Scientific inquiries into these questions have for decades worked under dichotomous philosophies called the ground-up or the trees-down hypotheses. Certainly, it seems easiest for flight to come from the trees and go through a series of baby steps using gliding morphologies to eventually produce a powered-flight outcome. This idea makes intuitive sense as a stepwise series of events known as gradual evolution. Therefore, the trees-down model of bird evolution seemed to clearly be the likely pathway. Then came the work of Dr. Ken Dial at the University of Montana, where he showed that young pre-flying birds use their wings for an amazing and previously unidentified behavior: climbing. Dial looked at how the youngsters of ground-dwelling birds, such as chukar partridges, that could not yet fly but flapped their wings vigorously, not to take air but instead to produce downward forces to aid in running up inclines or even vertical tree trunks to escape predators. The young birds were using the same wing-flapping angles as those used in flight for a very different type of behavior, which was to keep their bodies pressed against an inclined or vertical surface so they could easily climb with their legs. Astonishingly, the birds were doing the very opposite of flying by using their wings to push their bodies downward rather than lift them off the ground. Dial then found that any bird, adult or juvenile, if placed on a vertical post, climbed in the same manner rather than flying off the post. In other words, he could induce this behavior in adult birds, a remnant of their young nestling days. This suggested that the behavior was deeply wired into birds and probably had an ancient evolutionary history that may have pre-dated flight. Thus, wings and flapping evolved initially not for flight but to aid in vertical climbing. Not only that, but birds apparently did not go through gliding phases toward flight but instead evolved directly into flapping flight, giving credence to the ground-up hypothesis. Dial termed this newly discovered behavior "wing-assisted incline running" (WAIR).

Has something similar been found in bats? Not so far. But as with birds, two fundamental questions need to be answered. One, did bats evolve toward powered flight through a series of gliding phases, or did flight evolve directly with no intermediate gliding forms? Two, did bat flight evolve from an arboreal or a terrestrial ancestor? We know bats clearly came from a quadrupedal ancestor, as there are no known bipedal mammals that could be the ancestor of bats and because contemporary bats and their ancestors use all their limbs for walking and climbing. Thus, the puzzle is perhaps more difficult to solve for bats than for birds. Because the ancestor of birds was already bipedal and only required its rear legs to walk or run or climb, the forelimbs were left free to follow an evolutionary pathway independent from the rear legs. Quadrupedal bats were not so lucky. Similarly, though, bats have also been hypothetically put into the ground-up or trees-down paradigms of flight. I will say from my experience, however, that biology rarely conforms to dichotomies and instead typically operates in shades of gray. That said, the trees-down model appears on the surface to be the most likely hypothesis for bats because hanging from their rear limbs would free up their forelimbs for a somewhat independent evolutionary path. In addition, moving to various gliding stages (stepwise gradual evolution) seems very safe and logical, as it did for birds before Dial's surprise findings.

For those postulating that bats must have gone through a gliding stepwise evolutionary sequence, tree shrews that lived inconspicuously among the dinosaurs (figure 1.1) for decades were an attractive choice for an ancestral stage. However, nature above all else rarely follows human logic and most highly innovative evolutionary pathways go through maladaptive stages that have a high propensity for extinction. This is probably one of the reasons flight may be so rare in vertebrates, having occurred in only three known groups across 600 million years of evolution. Curiously, gliding is relatively common in mammals even though flight is not, but none of these gliding mammals show any "advancement" toward powered flight. In fact,

FIGURE 1.1. *A hypothetical Old World tree-shrew ancestor of bats in Eocene times (by Wendy Smith). Recent genetics suggests that the ancestor to bats may have resided in the New World among the extinct insect-eating terrestrial mammals of the Paleocene or early Eocene, 55–60 MYA, rather than with tree shrews. However, the origin of bats is still very much debated.*

it seems clear that the evolution of gliding locomotion is in itself its own evolutionary dead-end, and there is no evidence that it leads to powered flight. Even more profound, the functionality of transitioning from a gliding morphology to one used in powered flight is fraught with mechanical and functional problems and very unlikely to succeed. For example, if a flying squirrel attempted to flap its gliding membrane as it descended, it would drop like a rock. Add to this the fact that there are no fossils of intermediate stages between gliding and powered flight in mammals and it seems that the direct-to-flight hypothesis is more likely than the incremental gliding stages hypothesis. Furthermore, if a direct-to-flapping-flight hypothesis is correct, the ancestor to bats may have been terrestrial rather than arboreal.

Surely, if we ponder this a bit more, the Wright brothers did not push their airplane off a cliff, hoping to glide, and then start the engine. As reason prevailed, they determined that taking off from the ground would certainly be safer because if there was a miscalculation, fluttering to the ground would probably not be fatal.

Perhaps the trickiest question surrounding a terrestrial direct-to-flapping-flight ancestor is: why would webbed fingers evolve if not as gliding precursors to flight? The only mammals outside gliders and flyers with webbed feet are semi-aquatic ones, which are terrestrially based, not climbing-adapted, forms. But could they still be a possible evolutionary link? As it turns out, some contemporary shrews have webbed feet. Water shrews (*Sorex palustris*) of North America have webbed hind feet; the elegant shrew (*Nectogale elegans*) of Southeast Asia has webs on all four feet, is completely blind, and may use a primitive sonar system for navigation like some terrestrial shrews, possibly the precursor to bat echolocation.

So today, researchers are still uncertain from what ancestor such a spectacular mammal, with wings for cheating gravity and a voice allowing for navigation in complete darkness, originated. Furthermore, was this a onetime event, or were there possibly independent origins for bats across multiple horizons? For the most part, morphological analyses and genetic/molecular relatedness give conflicting results and therefore lack continuity. As a general evolutionary principle, clades of organisms (those sharing highly similar morphologies or genetics) are monophyletic, that is, having a single ancestral origin, representing a onetime walk-off event, and then diverging through time into distinctive but closely related species. However, complicating this premise is what is termed *convergent evolution*, wherein natural selection produces similar-looking organisms from vastly differing ancestry because the most adaptive forms for that environment share similar characteristics. For example, aquatic mammals show similar characteristics adaptive for efficient swimming, such as the smooth, streamlined bodies observed in all species of fish and in aquatic mammals such as dolphins and whales (cetaceans). Although cetaceans and fish do not share a direct common ancestor, these widely unrelated groups look very similar due to the fact that they live in an environment that selects for specific traits "required" for survival. Indeed, efficiently moving through water is difficult due to its density, and a nonadaptive body form would not likely survive competition for food with more adaptive forms. Similarly, flight encompasses a suite of unique adaptations similar across taxa as dissimilar as insects, flying fish, birds, and mammals because they are essential for survival. Therefore, if flight did evolve multiple times, this may be masked by the convergence of adaptive traits that anatomically group non-related species together simply due to the demanding physics of flight. Analogously, convergence can also occur molecularly/genetically, thereby giving a false impression of heredity and relatedness.

Whatever the case, powered flight is an amazing and rare adaptation for vertebrates; as mentioned, it appears to have evolved independently only three times ever. All three successful skyward reaches occurred autonomously and were separated by millions of years (figure 1.2). Birds, bats, and pterosaurs do not share a direct common ancestor that had wings; thus, their flight behaviors originated independently, in each case stemming from a unique series of momentary interactions among the genotype (within which mutation is the source of innovative form), evolutionary history (which determines who has what genes), and environment (which is the selective influence on gene products—i.e., form).

Pterosaurs (flying reptiles) were the first vertebrates to fly, appearing about 220 MYA. They witnessed the dawn of birds (~100 MYA) but saw their own demise during the Cretaceous extinctions 65 MYA, which also relinquished the dinosaur's grip on world domination. Fossils indicate that 52 MYA, bats were already bats, and these early denizens could easily be mistaken for contemporary species, indicating that the transition from terrestrial mammals to a fully flying one was much earlier by millions of years. The lack of transitional stages may also indicate very rapid evolutionary change, which lessens the likelihood of fossilization for intermediates. Among these early flying vertebrates, birds and bats were the only two-winged mammals to persist into contemporary times. Fossil evidence for the dawn of birds is inscribed in 100-million-year-old limestone sediment where fossils, such as the famous specimen named *Archaeopteryx* (as well as others), have been found. Having a horny bill while retaining a mouthful of teeth, *Archaeopteryx* was built of two worlds—one reptilian, the other avian—marking an important transition in evolutionary history. Curiously, although we associate feathers with birds, the evolution of feathers occurred in a group of theropod dinosaurs that were ancestral to birds and could not fly. Plumage, it turns out, graced terrestrial species before becoming airborne.

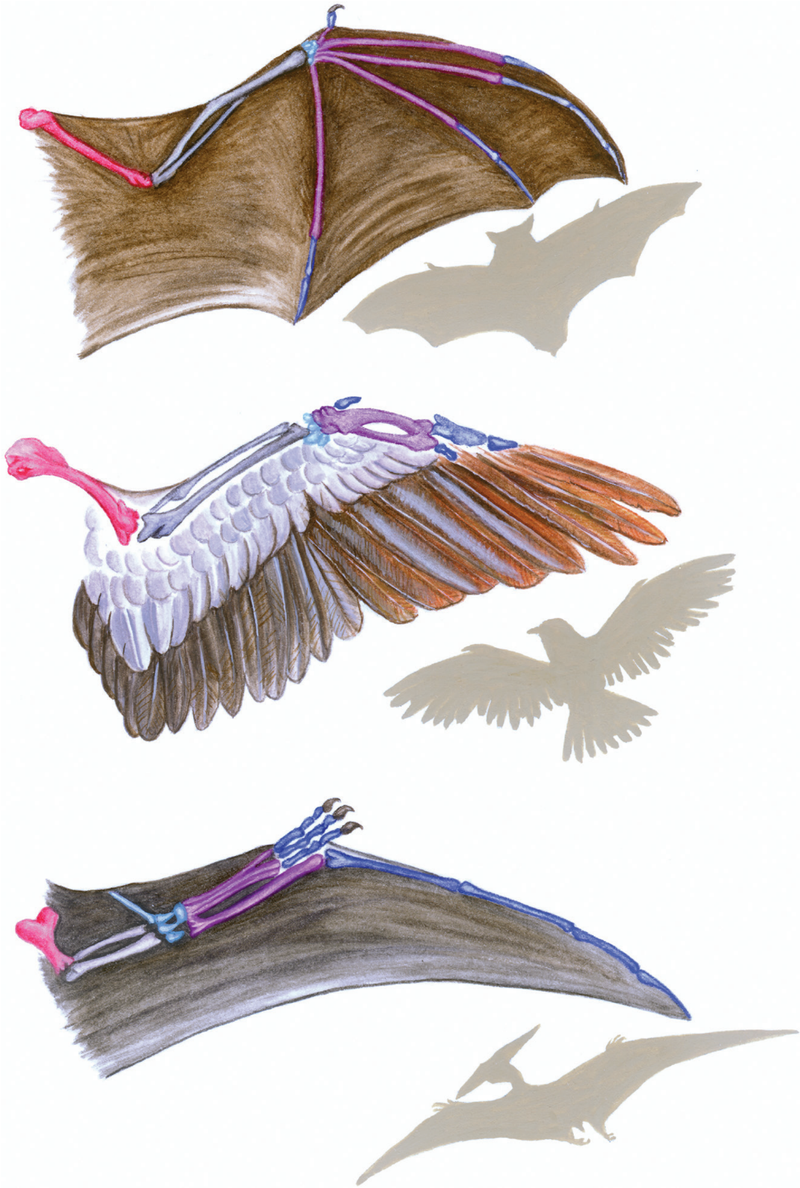

FIGURE 1.2. *The three types of wings evolved in vertebrates (by Wendy Smith). From top to bottom: bat, bird, pterosaur. Color coding illustrates the same bones across types.*

Bats were the most recent vertebrate group to evolve powered flight and were apparently the only mammal to succeed in flying or maybe even to try. Mammals themselves are descended from cynodont therapsids, an extinct transitional group that manifested both reptilian and mammalian characteristics and is therefore referred to as "mammal-like reptiles." It is here, in this transitional stage between reptiles and mammals, that hair evolved. Furred forms thus preceded winged forms (as feathers preceded flight in birds) by almost 180 million years, which means that bats have existed for a mere 25 percent of the evolutionary history of mammals.

After existing for 100 million years, mammals witnessed a major extinction event at the end of the Cretaceous period, 65 MYA, that extinguished approximately 76 percent of Earth's flora and fauna including the dinosaurs, prompting a major resorting of life. The dinosaurs that had trampled around the globe for more than 160 million years were forced to extinction, but many mammals survived and even prospered. In fact, after the Cretaceous mass extinctions, the ensuing mammalian radiations (explosions of species) changed the planet forever; for the first time in evolutionary history, fur came to dominate scales and feathers in terrestrial environments. Within the following geological eyeblink of 30 million years, all the major orders of mammals evolved, and one of the earliest groups to emerge from a burned and devastated world was bats. From these ignoble beginnings, bats came to witness firsthand the coming Age of Mammals, termed the Cenozoic Era. We may never know what the first protobat looked like, but from this spark of evolutionary innovation came the more than 1,480 species of bats that grace our planet today, specialized to take advantage of a mostly untapped food resource: night-flying insects. Further, night flight dramatically reduced the number of aerial predators for bats to navigate, and these combinations of traits propelled one of the greatest success stories in mammalian history.

The Structure of Bats

The structure of bats has changed little in the last 52 million years, and their anatomy at first glance appears unique but also familiar. For example, even though the wings are distinctive adaptations for flight, the overall skeleton, including the wing bones, looks unambiguously familiar. Composed of easily recognizable bones located in the same relative position as is present in all mammals, including humans, we can see that the same forelimb bones were

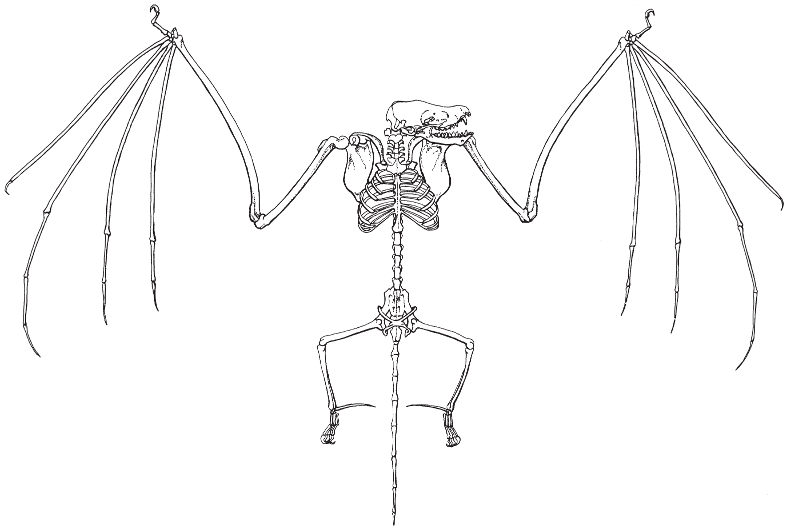

FIGURE 1.3. *Anatomy of a bat skeleton (Wendy Smith)*

simply elongated to make elemental supports for the wing membrane (figure 1.3). In fact, the basic anatomy of bats and other mammals is traced back almost 400 MYA to the dawn of the amphibians but has been elaborated on through bone fusions, reduction, or elongations of the basic ancestral pentadactyl (five-fingered) limbs we can recognize in all land vertebrates. Furthermore, we now know that the extensive elongation of the fingers in bats for flight is the product of a single gene mutation, and simply (or not so simply) transplanting this mutated gene to mouse embryos causes elongated digits in them as well.

But long bones are one thing. Bats also need webbing, or what is called a patagium, which actually creates the lift required for powered flight. So, the gracile and highly elongated fingers and forearms support a thin, elastic membrane (the patagium) that extends from the shoulder, travels between the digits, and reconnects along the body's lateral edge (figure 1.4). Interestingly, during development, mammals inherently begin hand formation as a webbed structure until a certain gene turns on and causes what is called apoptosis (literally, death of cells) and the webbing disappears as the limb grows. So, for bats as well as aquatic and many semi-aquatic mammals, this gene never turns on during growth and development, creating the possibility of flight and, of course, swimming.

FIGURE 1.4. *The patagium of a bat's wing showing the complex mosaic of mesh-like muscle fibers composing the wing membrane (Wendy Smith).*

The thumbs of bats appear deceptively small when compared to the other elongated fingers, but they are actually in proportion to body size. They are not involved in the flight membranes but instead function well as mechanical hooks for climbing, manipulating food, and grooming. The tail in most species is wrapped by a membrane, called the uropatagium, which stretches between the hind legs and tail, completing the flight surface. The uropatagium functions as a rudder during flight but is also employed in capturing insects that are then transferred to the mouth. Fascinatingly, slow-motion videography has shown that the uropatagium acts as a third wing when actively flapped asynchronously with the hand wings to help produce additional thrust when needed. All in all, the unique interlacing among supporting bones, elastic flight membranes, and flight muscles produces a

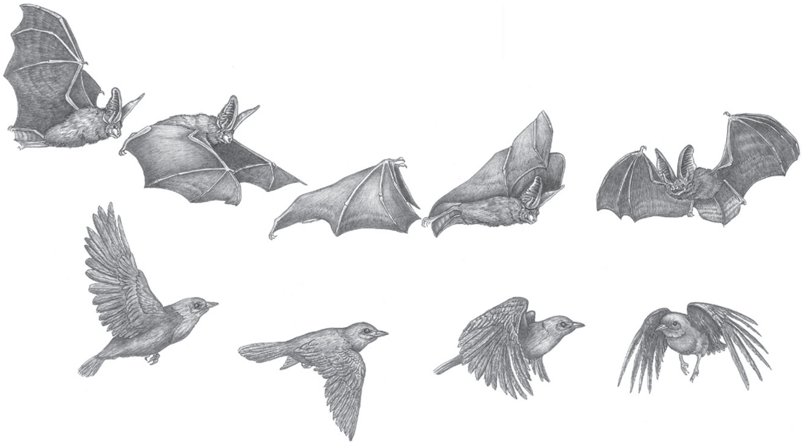

FIGURE 1.5. *Similarities and differences between flapping flight in bats and birds. Both use powerful muscles for flight, but in birds the downstroke is the only power-generating motion since the backstroke is passive because the feathers turn, allowing air to pass between them as the wing is pulled fully inward to the body. In bats, the wing is fully extended during the downstroke to lift the bat upward, as in birds. Unlike birds, however, the backstroke in bats creates forward motion because the patagium between the forearm and the body remains extended during the backstroke, whereas the patagium associated with the digits is collapsed as the hand is turned perpendicular to the ground to avoid downward forces. As the wing tip snaps backward at the end of the upstroke, this creates forward acceleration, as illustrated in the lateral and frontal views above (Wendy Smith).*

composite so dynamic that it allows some bats to zip into instantaneous 90 degree turns, sometimes at flight speeds approaching forty miles per hour. Don't try such a move in your Cessna.

Bats orchestrate flight in a unique manner compared to the only other living vertebrate fliers: birds. To capture and exploit the invisible matrix of air, bat wing movements are coordinated by using alternating contractions of both the chest and back muscles. The downstroke provides the force that cheats gravity, whereas the backstroke pushes them forward (figure 1.5). In contrast, birds manage flight in what might arguably be a simpler method that only employs their massive chest muscles. Contracting those muscles invokes a powerful downstroke that both lifts and accelerates birds through the air. The backstroke is passive and simply resets their massive chest muscle to refire. And so goes the differing physiques between these groups. Birds have more spherical body shapes, whereas bats retain a slender appearance by divvying up wing motions between chest and back muscles. This lean physique also gives them the ability to squeeze into small cracks and crevices to hide from predators. In addition, bats, unlike birds, have the distinctive ability to flap their wings not only synchronously but also independently of each other, making them the foremost acrobats in the sky.

At rest, bats hang upside down, remaining that way for up to seven months during hibernation. Unique cavities in the cranium pool blood and other fluids away from the brain. In animals not adapted for upside-down posture, such as humans, death due to brain tissue suffocation from pooling fluids would happen within eight hours. In addition, bats can hang passively from a perch without the assistance of leg muscles, even while sleeping, because the tendons operating the toes are scaly and pass through long cylindrical sheets of roughened tissue called sheaths. As the animal's weight pulls against the toes, it causes the scales on the tendons to embed into the sheath, locking the digits in position (figure 1.6). This "passive-lock system" allows the toes to remain in a gripping posture without the aid of muscle contraction. Disengaging the passive-lock system is achieved by contracting the calf muscles that release the tendons from their sheaths. So, roosting bats hang effortlessly; in fact, the passive system works so well that bats long dead are occasionally found still hanging in their roosts. Curiously, a similar but unrelated passive mechanism has been found in the feet of perching birds.

Bats have large hearts for supplying ample amounts of blood to oxygen-needy flight muscles. Their hearts are also speedy, generating a resting (basal) rate of about 450 beats per minute, which is 2.5 times that of a conditioned athlete while running. Although that value is amazing in and of itself, the magic really begins when bats fly, as their heartbeat approaches 20 beats per second, or 1,200 beats per minute. Perhaps even more impressive is a bat's control over its racing heart, which returns to a basal rate within seconds after landing. Again, even well-conditioned athletes would require ten or more minutes to fully recover after a run.

Because of such accelerated metabolic rates during flight, bats require high-energy, abundant food resources. Consequently, most of today's species consume a calorie-rich diet consisting of insects, fruit, or nectar; their teeth are adapted for efficient mastication of their primary food source (figure 1.7). In fact, because the form and function of teeth so clearly depict a mammal's diet, understanding the evolutionary past of bats is enhanced

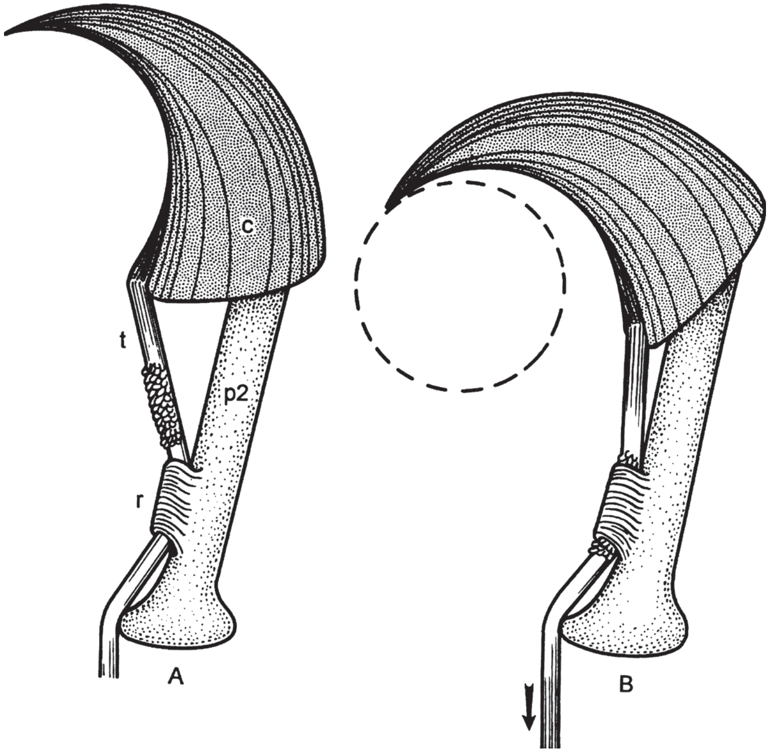

FIGURE 1.6. *The passive-locking mechanism in the feet of bats that allows them to hang effortlessly during roosting (from Schutt 1998)*

by the study of dental characteristics, allowing for hindsight back through many millions of years. Furthermore, because teeth are the hardest biological substance and are capable of surviving long expanses of time, they are invaluable materials to paleontologists. The discovery of ancient fossil bat teeth places their ancestry firmly within a group of mammals that witnessed the demise of the dinosaurs 65 million years hence, followed by an explosion of mammalian forms that radically altered the ecology of life on Earth. Indeed, one of the first groups to arise from the stock of late Cretaceous mammals was bats; through time, they speciated extensively.

Bats Today

Bats are classified in the order Chiroptera, a term meaning "hand wing." The order is subdivided into suborders termed the Microchiroptera (i.e.,

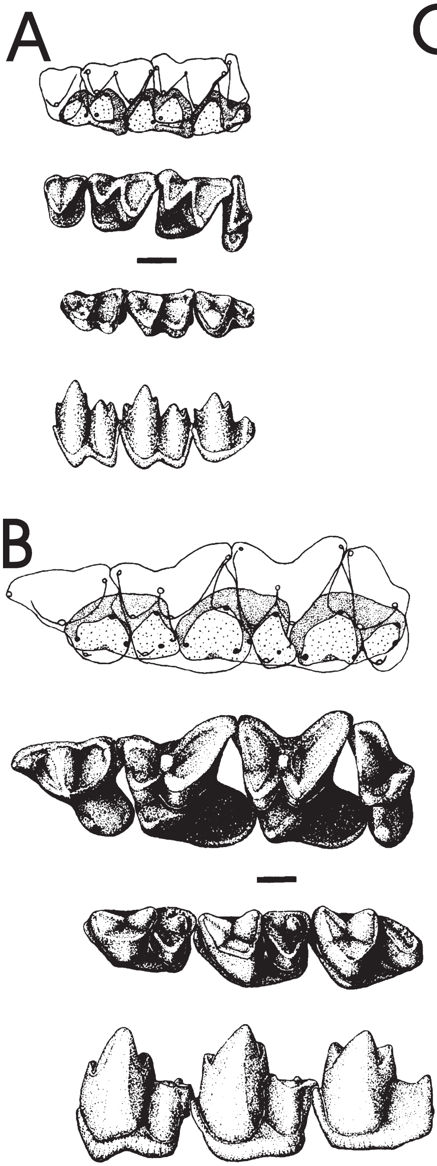

FIGURE 1.7. *Various tooth morphologies of bats that strongly correlate with a species' diet: (A) the insectivorous* Antrozous pallidus, *(B) the carnivorous* Macroderma gigas, *(C) the nectarivore* Monophyllus redmani, *and (D) the frugivore* Artibeus jamaicensis *(from Freeman 1998).*

FIGURE 1.8. *A Mariana flying fox (*Pteropus mariannus*) taking the fruit of a fagot tree (*Neisosperma oppositifolium*) on the Island of Guam. Flying foxes in the family Pteropodidae have uniquely large eyes capable of color and binocular vision adapted for crepuscular foraging. They also have elongated and clawed opposable thumbs for manipulating fruits. These bats also have a claw on their second digit. These characteristics are not found in other families of bats. (Merlin Tuttle, with permission)*

microbats), meaning "small hand-wing bats," and the Megachiroptera (megabats), meaning "large hand-wing bats." The megachiropterans occur solely in Old World regions such as Africa, India, Australia, and Indonesia and include only one family, the Pteropodidae, whereas microchiropterans occur worldwide except on the continent of Antarctica. Some genetic analyses have suggested reordering bat taxonomy into the suborders Yinpterochiroptera, which includes the megabats plus two families of microbats, and Yangochiroptera (all other microbats); however, the morphological connectedness challenges this arrangement. Whatever the outcome taxonomically, the pteropodids are commonly referred to as flying foxes due to their doglike facial features (figure 1.8), and these bats comprise about 190 of the 1,480 estimated total bat species. They are not particularly diverse morphologically or ecologically, as they are either fruit eaters or nectar drinkers (or both). Pteropodids locate fruiting trees using their excellent sense of smell and vision, and none are known to use ultrasonic sonar; curiously, one species in the genus *Rousettus* does use audible tongue clicks as a primitive form of echolocating when moving through caves. The majority of species appear to have color vision. Although pteropodid bats range in size from about 15 grams (0.5 ounces) to 1.1 kg (2.4 lbs), most of them are near the larger end of this spectrum with the record currently held by the giant Malayan flying fox, with a wingspan reaching 1.8 m (~6 ft). Its scientific name, *Pteropus vampyrus*, falsely indicates a blood-sucking intent; in reality, this species eats fruit.

All other bats, ~1,290 known species, are classified into twenty families of mostly smaller-bodied insect- or fruit-eating species. They are much more widespread than the pteropodids, occurring on all continents except Antarctica. Ecological diversity of microbats is phenomenal, including those that feed on fruit, nectar, insects, rodents, birds, fish, frogs, and blood. The species that feed on other vertebrates tend to be large, with up to 1.2 m (~4 ft) wingspans (figure 1.9). One of the more specialized vertebrate eaters is the fishing bats, of which there are two species in the Neotropics. These bats fly along streams hooking fish at the surface using large, curved claws on their hindfeet (figure 1.10).

Among the most peculiar bats are vampire bats, of which there are three species living only in Neotropical regions. Two species, the hairy-legged vampire (*Diphylla ecaudata*) and the white-winged vampire (*Diaemus youngii*), hunt mostly for the blood of birds, whereas the common vampire bat (*Desmodus rotundus*) lives only on the blood of mammals. Despite humans' revulsion toward any animal that feeds on the blood of others, vampire bats represent a pinnacle of natural selection and evolutionary success. Biases aside, these bats manifest a suite of characteristics that make them extraordinary. Specialized razor-sharp incisor teeth allow vampire bats to nick and penetrate the very thick hide of mammals and scaly legs of birds quickly and efficiently. Once a small incision is made, saliva containing an anticoagulant is drooled onto the cut, keeping the wound open and bleeding. A tube-like structure on the back of the tongue assists in moving blood to the mouth, like a straw. Once full of blood, the stomach becomes so distended and heavy that flight is difficult due to the excess weight, hence the name of the common vampire, *D. rotundus*. The fact that they have the shortest gastrointestinal tract of any living mammal allows vampire bats to digest blood very quickly, excrete the excess water, and fly off a few minutes later.

FIGURE 1.9. *False vampire bat or spectral bat (*Vampyrum spectrum*) with a bird, a white-collared manakin (*Manacus candei*), in Costa Rica. These carnivorous bats are the largest bat in the New World (1.2 m [~4-ft] wingspan) and commonly ambush prey from stationary roosts. (Merlin Tuttle, with permission)*

Furthermore, even though these bats have effective night vision and echolocation, they also use heat pits positioned on each side of their nose that are capable of detecting minute temperature changes from several feet away, helping them locate warm-blooded prey in complete darkness. These heat pits also aid the vampire in choosing where on the host's skin to make an incision. Before cutting, the bat first slides its heat-sensitive pits along the prey's skin to determine where the blood vessels lie closest to the surface. This ensures that the bat avoids wasted time cutting in areas where blood is

FIGURE 1.10. *A fishing or bulldog bat* (Noctilio leporinus) *catches a fish from a pond in Costa Rica with its specialized hooked claws. (Merlin Tuttle, with permission)*

not easily available. Further, whereas most bats are not great at supporting their body weight when walking, vampire bats can run and jump with ease and tempo, having robust and explosive limbs (figure 1.11).

Visual Acuity, Sound, and "Seeing" in Darkness

The saying "blind as a bat" probably comes from the fact that many species tend to have smallish eyes; therefore, it seems that they would not be able to see well, if at all. In truth, all bats can see, and many have very good vision, although it is based predominately on low-light–sensitive rods. A 2010 study by Canadian researchers found that the abilities of little brown myotis (*Myotis lucifugus*) to avoid flying into stationary obstacles varied under different lighting conditions, showing that they were navigating by sight rather than echolocation, with most collisions occurring under higher illuminations. We have all seen or experienced trying to catch a ball when the sun was in our eyes. So, all eyes can be overwhelmed; it's just that most bats are tuned to much lower light sensitivity than are humans. In another captive study, blindfolded bats rarely collided with windows, whereas non-blindfolded bats commonly did, again showing the use of sight over echolocation under lighted conditions. Thus, it seems that bats use vision more than previously thought, but this makes sense energetically because producing sound takes a lot more energy than passively using light waves from the environment.

FIGURE 1.11. *A common vampire bat (*Desmodus rotundus*) leaps into aerial flight, thereby showing the powerful ability of its leg muscles (Merlin Tuttle, with permission).*

Amazingly, some bat species also have color-sensitive cones and can even see ultraviolet (UV) light, which is most abundant at dawn and dusk. It has long been thought that some Old World flying foxes (Pteropodidae), who cannot produce ultrasonic echolocation, have dichromatic color vision that allows them to see in the blue-green, but probably not the red, spectrum. However, genetics studies on opsin genes that evolved in support of color vision showed that middle- to long-wavelength (M/L) genes in flying foxes are functional and should allow for red-spectrum vision adaptive for finding fruit in low-light conditions. In fact, one of the species tested, Fischer's pygmy bat (*Haplonycteris fischeri*), sports a recent duplication of the M/L opsin gene (the only known case outside of primates), thereby providing new genetic material for further mutations of this gene that could expand the spectrum of color vision even more in future generations. In addition, an echolocating insect-eating bat species (*Myotis velifer*) in the study showed functionality in both the M/L opsin gene and the short-wavelength (S opsin) gene responsible for blue-spectrum detection. Curiously, the S opsin gene appears to have been evolutionarily lost in most nocturnal primates but has been retained in ultrasonically echolocating bats, in which it may allow for sensitivity of ultraviolet (UV) light. For many years it was thought that echolocating bats only had black-and-white rod-based (monochromatic) vision. While this may be the predominant visual acuity for many species, color vision appears to be maintained at least on a functional genomic basis, with the addition of UV sensitivity, which is rare in mammals. Until we have devised ways to actually see through the eyes of another species, accurately understanding their visual perception of the world will remain somewhat based on conjecture.

Whatever turns out to be the truth about color detection abilities in bats, vision is not an optimal sense for nocturnal animals, as all vision requires some light, which may be nearly absent on moonless nights. Even though we humans pride ourselves on having a good sense of sight, most of us would not run through the woods at night without a flashlight or perhaps even with one. Not surprisingly, evolution has favored the use of sound for nighttime navigation and prey acquisition in bats, as well as some other mammal species such as porpoises, whales, rats, and shrews. However, bats appear to have the most complex sonar systems to have evolved wherein they emit high-frequency sounds from their larynx as loud as 120 decibels, which bounce off all objects in the environment as echoes that return to the bats' ears where the signals are translated into neuron activity that the brain must decipher in milliseconds when in flight (figure 1.12).

The scientific inquiry into bat sonar is an exemplary model of the scientific method at work. Early investigators were shocked to observe that bats could fly in complete darkness while avoiding collisions with wires as thin as a human hair. Lazaro Spallanzani hypothesized that bats use a method other than vision by which to navigate. He performed experiments on bats using, first, hooded and, later, surgically blinded individuals. Through a series of letters to colleagues, he inspired surgeon Louis Jurine to replicate his experiments and to further explore the phenomenon by plugging the ears of some bats. Jurine found that deafening bats resulted in confusion and disorientation. He sent his results to Spallanzani. Bewildered, Spallanzani and Jurine continued to collaborate. In a flash of insight, in 1799 Spallanzani wrote his hypothesis that "the ear of the bat serves more efficiently for seeing, or at least for measuring distance, than do its eyes, for a blinded animal hurtles against all obstacles only when its ears are covered . . . Can it be said then that . . . their ears rather than their eyes serve to direct them in flight?" Spallanzani

FIGURE 1.12. *The workings of echolocation. High-frequency sounds emitted from the bat's larnyx (red semicircles) travel away. Upon contact with objects in the environment, the sound waves bounce back to the bat's ears in the form of echoes (yellow semi-circles). The bat's brain interprets these sounds as three-dimensional portraits of the objects present in its flight path (not unlike the way the human brain interprets light waves). (Merlin Tuttle, with permission)*

and Jurine predicted that bats oriented themselves primarily by using self-generated sounds. Unfortunately, their unpublished investigations and ideas generated little interest in the scientific community and subsequently fell into the abyss of "unattended concerns." Thus, in spite of Spallanzani's and Jurine's carefully controlled experiments and marvelous insights, the concept of "seeing with ears" was too mentally challenging for many to accept. Some scientists, such as G. Montague, after reading Spallanzani's and Jurine's results, stated: "To assent to the conclusions of Mr. De Jurine . . . since bats see with their ears, do they hear with their eyes?" In the nineteenth century, paleontologist and anatomist Georges Cuvier rather cavalierly decided that bats oriented themselves using a specialized sixth sense (one of Spallanzani's early hypotheses) that emitted from their wings and was undetectable to humans. Due to Cuvier's fame, this scientifically unsupported idea propagated throughout the world, even spilling over into the twentieth century.

It was not until the 1930s that the puzzle of bat orientation was revisited and subsequently solved. Spallanzani and Jurine's well-reasoned suggestion of ultrasonic orientation aged like a fine wine for nearly two centuries before it was uncorked by biologist Donald R. Griffin. Working on a hunch and intrigued by the Spallanzani/Jurine hypothesis, Griffin brought some bats to a physicist's laboratory that had an instrument capable of detecting high-frequency, or ultrasonic, sounds. He wrote, "With some trepidation I approached Professor Pierce in the winter of 1938 with the suggestion that we use his apparatus to listen to my bats." Upon entering the room with the bats, the scientists became the first humans to hear a series of sounds that may have first been made when dinosaurs still roamed the earth. Griffin (1958: 67) wrote, "When I first brought the cage full of bats [*Myotis lucifugus* and *Eptesicus fuscus*] to Pierce's laboratory and held the cage in front of the parabolic horn we were surprised and delighted to hear a medley of rancorous noises from the loudspeaker." Griffin coined the term *echolocation* to describe this ultrasonic cacophony, and the word is descriptive of how he envisioned bat sonar to function. He hypothesized that bats emit high-frequency sounds from their mouths and utilize their ears to gather the returning echoes to locate objects and to navigate.

Curiously, even before Griffin's discovery, the study of bats led humans to have insights that resulted in inventive technological advances. As early as 1912, inventor Sir Hiram Maxim proposed that bats navigate by emitting low-frequency sounds (infrasound) and thus hypothesized that humans could construct devices to work similarly for navigating ships in darkness. In 1920, English physiologist Henry Hartridge proposed that bats use high-frequency sounds (ultrasound). This, of course, was what came out of the Griffin/Pierce experiments.

In a sense, Griffin's discovery of echolocation was the easy part. After all, we humans simply waited for technology to provide the instrument that would allow us to detect what bats have been hearing for millions of years. Deciphering exactly how echolocation works proved to be the real challenge. Despite the involvement of hundreds of biologists conducting thousands of experiments and rigorous investigations since Griffin's discovery, a thorough understanding of how echolocation works and is interpreted by bats remains elusive.

Human radar and sonar systems were developed from a basic understanding of bat, as well as cetacean, biosonar systems; in comparison, these human devices are rather crude. Yes, you can probably blame, at least indirectly, that last speeding ticket you received on the study of bats. But the sonar of bats has also given us important devices such as ultrasonic orientation systems for the blind and ultrasound imaging to see and investigate our unborn children.

We also know today that echolocation in bats is not a simple navigational and prey-finding sound system. Instead, ultrasonic calls in bats are rich in social information, including species identification, sex, age, body condition, reproductive condition, group and/or individual identity, and other information not yet deciphered by human investigators. Because bats emit what is termed a *feeding buzz*, a series of rapid echolocation pulses reaching 200 per second, foraging bats can also eavesdrop on each other's echolocatory pulses to find the best hunting grounds in the area.

Amazingly, although bats clearly use echolocation for hunting and navigation, we now know that ultrasound is full of information about the individual as well. Just as we can tell each other apart by our voices, so can bats distinguish each other. Furthermore, information on individuals' emotional state is also imbedded in bats' highly complex vocal resonations. The social interactions and complex soundscapes produced by bats are only beginning to be studied in ways designed to interpret what they are talking about. In-roost social calls can be observed in captive colonies and sometimes in natural roosts and then be tied to an individual's behaviors, which may give some insight into their meanings. Calls between mothers and pups involve specific forms termed *repeated trills* or *curved cheeps* that are repeated by pups in their mothers' absence; their mothers use the same calls to find them when they return to the colony. Among adults, "sqauwks" are commonly accompanied by threat displays and therefore are recognized as an antagonistic communication. Other calls that have been recorded and displayed as having "humped," "wrinkled," and "sinusoidal" patterns appear associated mostly with mate attraction. Of course, as in humans, context is important, so similar sounds may have different intents under different conditions. As is nearly always the case in biology, once one starts to dig into specific questions with well–thought-out experiments, more questions are raised than answered, and we begin to understand our limitations in unpacking what can only be described as hyper-complex communication and social systems among highly intelligent beings.

Further Fundamentals of Echolocation: Seeing with Ears Is Not as Easy as It Sounds

Because the earliest fossils of bat skeletons indicate adaptations of the ear that are specific to echolocation in today's bats, it is assumed that these early batty renditions used echolocation in much, if not exactly, the same manner as contemporary species. In addition, the teeth of these fossil bats were for masticating insects, as are those of insect-eating bats (and shrews) today. Thus, it appears that these early bats were already nocturnal and hunting night-flying insects, thereby apparently operating in much the same way 52 MYA as are the bats flying around your house on summer nights.

Both molecular and morphological studies taxonomically place echolocating bats as evolving from a group of mammals called laurasiatherians, which includes terrestrial shrews, carnivores, ungulates, and others. Curiously, it has been shown that shrews use a primitive ultrasonic sonar system to navigate and hunt, which provides a viable alternative hypothesis that microchiropteran bats inherited a primitive echolocation system from a shrew-like ancestral protobat rather than invented one themselves. Over time, this primitive echolocation system became more derived into the complex sonar capacity of today's bats. Indeed, studies of the ontogeny (growth and development) of echolocation in bats indicate that not only does ultrasonic sound production develop independent of audible sound production in infant bats but also that adult-level echolocatory aptitude develops long before the flight ability of young bats comes online. This suggests that the evolution of echolocation preceded the evolution of flight in bats.

Whatever the case, bats are a product of integrated evolution and development among several anatomical systems—including the brain, auditory, cardiopulmonary, visual, vocal, olfactory, and skeletomuscular systems—that merged in an extraordinarily unique way. It is surmised that the basic integration of anatomy, physiology, and behavior occurred quickly at the dawn of bats. Once the basic integration was established, fine-tuning of what was likely an initially crude system was surely a priority because echolocation requires a high-energy investment, and species that waste energy are usually doomed to become what famed entomologist Edward O. Wilson termed "Darwinian wreckage" along the evolutionary highway—which was absolutely not the case for bats.

Echolocation Pulse Rates: Speed Kills

One refined aspect of echolocation seen in today's bats concerns phasing the call speed differently to help conserve energy while foraging (figure 1.13). When searching for food, the pulse rate is slowest, at about 25 pulses per second; upon approaching a potential food source, the pulse rate doubles to

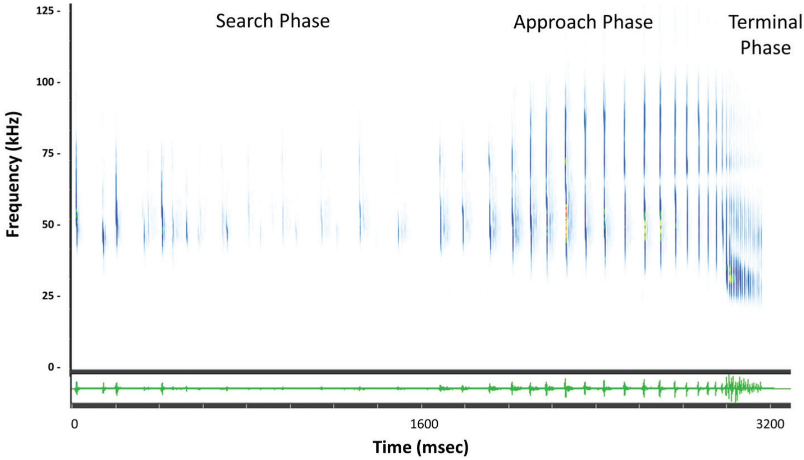

FIGURE 1.13. *Spectrogram of long-legged myotis (*Myotis volans*) pulse phases that increase in rate from search, approach, and terminal (also referred to as a feeding buzz) to lessen the overall energetic expense of echolocation. Reading this graph from left to right, increased pulse rates are indicated by the more closely packed lines. The vertical axis shows call frequency in kilohertz (kHz) (humans can hear sound up to about 20 kHz), whereas the horizontal axis indicates time in milliseconds (ms).*

about 50 pulses per second; and only when a strike is imminent do bats use their most sensitive call rate, which reaches 250 pulses per second. Referred to as a "feeding buzz" due to the buzz-like qualities of the sound, this terminal phase of echolocation gives bats detailed information about the prey's position, flight speed, and direction of movement. The energy saved by using different call rates is significant when the search phase requires one-tenth the energy of the feeding buzz. Both the search and the approach phases lack discernment, and bats in this phase of echolocation can actually be fooled into approaching a nonfood item (for example, a pebble thrown into the air). However, once the highly discriminatory feeding buzz engages, the pursuit usually ends because the bat usually realizes its mistake. Curiously, bats appear to have an innate understanding of the speed of sound. In an elegant experiment, researchers flew adult and juvenile bats in an environment containing Heliox gas (a mixture of helium and oxygen) that increases the speed of sound by 15 percent, thereby making a target appear that much farther away than it would in normal air. They found that neither adults nor juveniles could learn to adjust for the increased perception in target distance, thereby indicating that bats are born with an innate inalterable

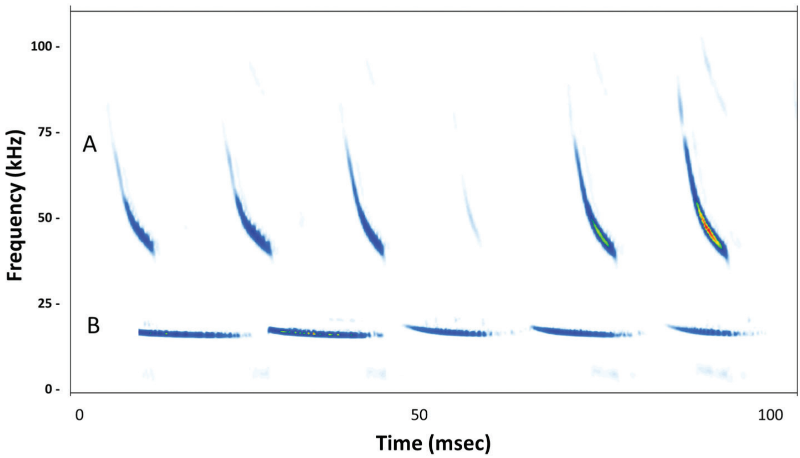

FIGURE 1.14. *Illustration of two types of echolocation calls. (A) Frequency-modulated (FM) call sequence of the California myotis (*Myotis californicus*); (B) a constant-frequency (CF) call illustrated by a spotted bat (*Euderma maculatum*).*

understanding of the speed of sound that appears to be hard-wired and not learned.

CF versus FM Bats and the Duty Cycle: Changing the Channel Is Not Optional for Most

Although the pulse-rate patterns discussed in the previous section are consistent across bat species, there are fundamental differences in the use of tonal frequencies, depending on a species' foraging strategy. Some species are termed CF bats because they use mostly constant, or relatively invariant, call frequencies (figure 1.14). Constant-frequency (or quasi-constant-frequency for those showing a slight change in the slope of their calls) sonar is associated with bats that forage for aerial insects in open areas using higher flight speeds. Because CF calls have relatively low discriminatory power, CF bats tend to search for insect clouds that they then fly through, mouth agape, filtering insects from the air. Free-tailed bats (such as the Brazilian free-tailed bat, *Tadarida brasiliensis*) hunt in this fashion.

Other species of bats use frequency modulation of the sonar call and are referred to as FM bats. These bats vary the frequency throughout the call sequence. Invariably, the call begins as a high-frequency pulse and ends at a lower frequency, sweeping through intermediate values. The big brown bat

(*Eptesicus fuscus*) is an example of an FM bat. It begins each echolocation sequence as high as 100 kilohertz (kHz), but each pulse is swept downward to about 20 kHz, thus increasing detail about prey items hunted. FM bats typically catch insects in flight by isolating individuals, pursuing them, and catching them with their flight membranes. Frequency modulation occurs throughout all phases of echolocation and is typically accompanied by two or three harmonics that give a highly detailed three-dimensional picture of insects flying in cluttered environments. FM bats are thus well suited for foraging in complex habitats and feeding on evasive insects. Many bat species use echolocation, which combines the qualities of both CF and FM pulse types, and some species vary their modulation type according to foraging habitat.

Recently, it has been suggested that CF versus FM echolocation may not distinguish bats as well as once thought because many species use both types of call strategies under differing conditions and even integrate the two types normally. The terms therefore serve more to describe calls rather than the bats using them. Some bat biologists, such as M. Brock Fenton, have suggested that "duty cycle" (the proportion of time a signal is in use) is a more discerning component of echolocation. Some bat species use a low–duty-cycle call in which the signal is on a mere 10 percent of the time because these bats cannot simultaneously broadcast pulses and receive echoes. Other bats emit high–duty-cycle echolocation calls in which the signal is on more than 30 percent of the time. These species are capable of broadcasting signals and receiving echoes simultaneously. Although the duty-cycle dichotomy appears to hold well across bat species, most biologists believe that describing bats solely by their call type in any way is misleading without adding information such as call duration, time between calls, call intensity, and presence or absence of harmonics. Although these components of echolocation can be broadly assigned to certain species, some species have high plasticity that allows them to alter echolocation parameters depending on the habitat in use. For example, controlled experiments offering open and cluttered habitat spaces showed that juvenile little brown myotis (*M. lucifugus*) used calls that were relatively longer and lower in frequency and had shallower slopes than calls they used in a more cluttered habitat. In what seems a rare display of intentionally using sonar in a somewhat cutthroat manner, Brazilian free-tailed bats (*T. brasiliensis*) attempt to jam each other's feeding buzzes when in competition for insects.

Nature's Arms Race: The Insects Fight Back

It may seem that bats have all the advantages when hunting insects, but that is not always the case. In fact, the coevolution between insectivorous bats and their prey is a fascinating story that can be characterized as a 52-million-year-old arms race. In response to the evolution of echolocation in bats, insects have evolved some amazing countermeasures to lessen their chance of becoming prey. In one of the more interesting cases, some moth species have evolved "ears," termed tympanic regions, on their thorax or abdomen that are specially tuned to the echolocation frequencies of foraging bats (figure 1.15). When an "eared" insect becomes targeted by a bat's feeding buzz, its thorax vibrates, telling the moth to begin evasive maneuvers. In sphinx moths, the tympanic organs not only allow detection of feeding buzzes but actually generate a signal that either warns an approaching bat that the moth tastes bad or, in some species, emits a signal-jamming sound meant to confuse the pursuing bat. The interactions between bats and their insect prey in many ways mimic an aerial "dog fight" (figure 1.16). As selection favors adaptations that increase the abilities of each species, this escalates efficiency among the species involved in the "arms race." Evolution has favored fast, maneuverable flight and echolocation in bats, whereas in moths, the abilities to eavesdrop on approaching bats and to engage in other evasive behaviors have been favored. When all is said and done, the evolution of ears in moths and some other insects results in a 2–5 percent increased success rate in avoiding predation by bats. Although these savings seem minuscule, in reality this increased survivorship ensures that moth populations will persist despite heavy predation by bats. The evidence that bats are responsible for the evolution of ultrasonic ears in some insects is compelled by the discovery that some tropical butterflies that have uniquely become nocturnal have evolved bat-listening ears. In addition, it is curious that some species of praying mantises, which are currently diurnal, actually retain bat-sensitive abdominal ears from a time long ago, when they were apparently nocturnal and perhaps "driven" to daytime activity to escape predation by bats.

Reproduction and Development: One Is the Loneliest Number

The reproductive biology of bats is fascinating, and we have barely scratched the surface for most of the 1,480 species. One of the largest misconceptions about bats is that they have many young a year, similar to mice. But nothing

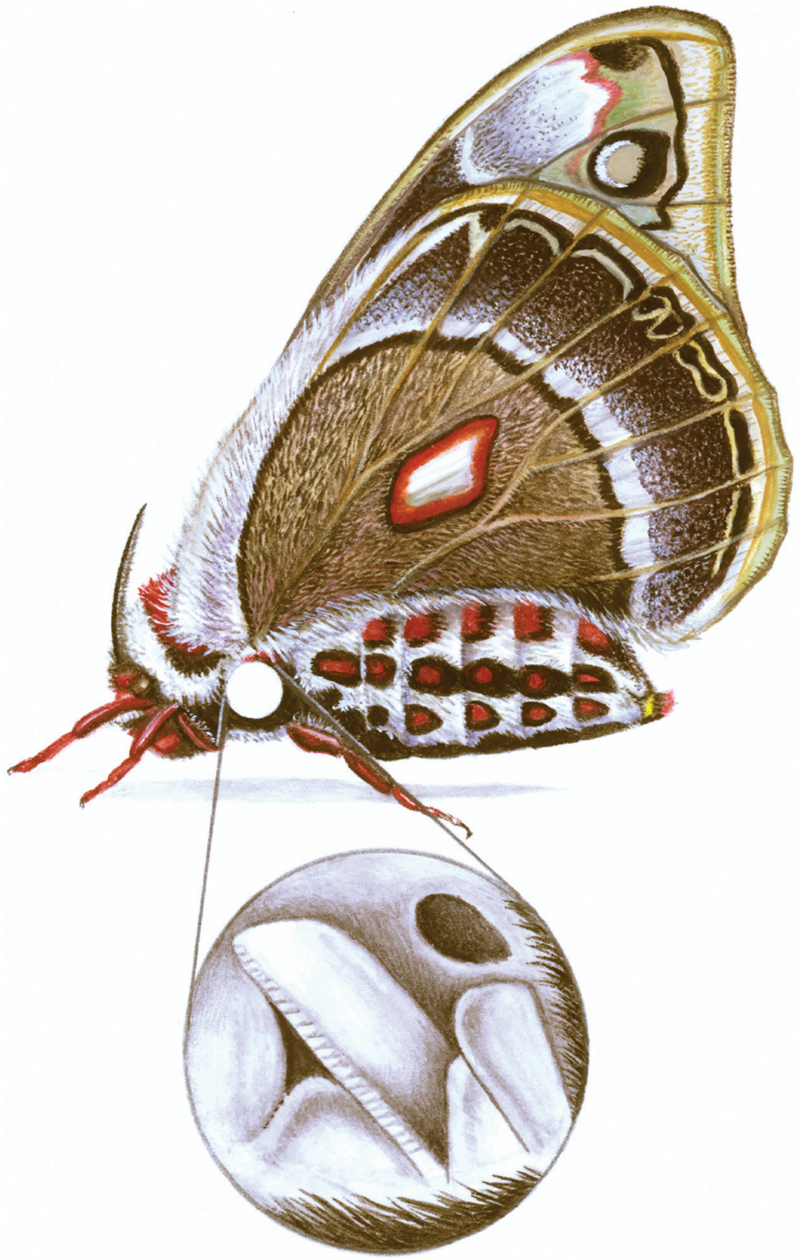

FIGURE 1.15. *The tympanic ear and organ (magnified) of an arctiid moth adapted to hear the ultrasonic terminal feeding buzz of bats. Upon stimulation, the insect changes its flight maneuvers to avoid predation or makes confusing ultrasonic clicks (Wendy Smith).*

FIGURE 1.16. *Avoidance behavior by a moth with a tympanic ear that has heard the feeding buzz of an approaching bat (Wendy Smith).*

can be farther from the truth. Most bat species have a single young per year, and this priceless bundle of time and energy experiences a high likelihood of survivorship while being cared for in the maternity colony. But once the young are fledged, mortality can skyrocket, and many juveniles do not make it through their first year. Therefore, bat populations are typically very stable and unchanging over time. However, if a population crashes, it can take decades for it to recover, if it does at all.

Reproduction itself is an intricate and complex amalgamation of behaviors, endocrinology, physiology, mating, genetics, cell division, sex, fertilization, development, and growth, as well as many ecological and evolutionary feedbacks. Because bats are so difficult to view in nature without human interference and disruption, data gathered thus far on many species are from those that have over time become habituated to humans by living in their buildings. But even this small sample shows that when it comes to the biological holy of holies, bats show wide reproductive plasticity among species and even among geographically different populations of the same species.

One of the most unusual stories in nature is observed in many North American bat species, including in the Rocky Mountain West. Seasonally induced impulses have males and females copulate up to six months before females even ovulate. In late autumn, females and males mate at specific locales after dark, called swarming sites, located outside a hibernaculum. Although mating ensues, fertilization cannot take place because females do not ovulate an egg that night or even over the following several months. In fact, ovulation does not occur until spring, after the two mates have slept off the winter blues and aroused to migrate to their summer haunts. How can this be? Sperm is known to be killed by body heat in endotherms relatively quickly (the very reason testes are located outside the body during the time of spermatogenesis), so how can the sperm survive inside the uterus of female bats for months? This type of reproductive pattern is very rare in mammals and is called delayed fertilization. We do not know exactly how bat lovers pull this off, but researchers think the females, which store the sperm that imbeds in the lining of the uterus (endometrium) throughout the over-wintering period, can do so only because in hibernation their body temperature is about that of a refrigerator, thereby allowing the sperm to be stored safely. In an amazing display of crowding, thousands of sperm line up along the uterine wall during hibernation and are drawing stored energy from the female to stay viable (figure 1.17). In spring, females come out of hibernation and ovulate an egg as sperm is released from the uterine lining and swims into the fallopian tube to fertilize an ovum. The fertilized egg then floats into the uterus and becomes implanted, where it develops into an embryo that is born as a pup fifty to sixty days later. Other modes of reproduction found mostly in tropical bat species include what would be considered the more normal mode in mammals—with immediate fertilization and implantations, delayed implantation where fertilization occurs but implantation into the uterine wall is impeded for some time, and embryonic diapause where fertilization and implantation occur but the embryo ceases to develop further until a specific chemical signal is received. The latter usually occurs in species that have more than one young a year, with each having different but usually overlapping gestation periods.

In terms of mating behaviors that have been studied, they are highly variable as you might expect by now. For example, in horseshoe bats (family Rhinolophidae), a common group of bats in Europe and Asia, it has been shown that echolocation calls—which, as mentioned, were previously

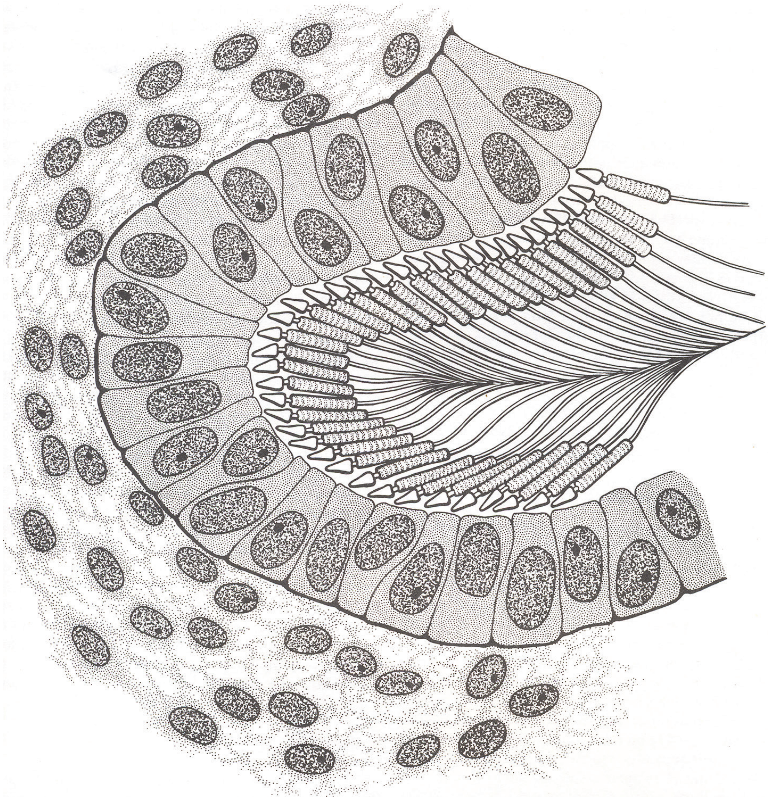

FIGURE 1.17. *Illustration of how sperm align and embed in the uterus of female vespertilionid bats after copulation in autumn and are stored there for up to five months (from Hill and Smith 1984). This process is termed sperm storage, which is very rare in mammals. The sperm will be released in the spring after females arouse from hibernation and are ready to ovulate an egg.*

assumed to be only for detecting food and obstacles—also give information on male body sizes. Females, it turns out, mate more with males that are larger and emit higher-frequency calls that give them away. Such males therefore sire more offspring than do smaller males. It is even thought that the extraordinarily high-frequency echolocation emitted by rhinolophid bats, previously thought to be entirely for catching insects, instead is most likely driven by mate choice and not by predator-prey coevolution. Curiously, it has also been shown in this family of bats that related females share and mate with the same males.

For most of the Rocky Mountain West bat species, there appear to be no overt mating rituals, and how mates are chosen is unknown. Some have hypothesized that mating is random, but this seems unrealistic in such an intelligent and sophisticated animal. One regional species, the California leaf-nosed bat (*Macrotus californicus*) that occurs in western and southern Arizona as well as in California, does show overt mating rituals (see Accounts of Species in chapter 6). Males find a particular spot in a cave and defend it from other males; as a female flies by, the male flaps his wings vigorously and vocalizes, trying to prod her to land in his pad. Such displays are commonly referred to as lek mating systems and are observed in many of the New World leaf-nosed bats of the family Phyllostomidae throughout the Neotropics, for which this species is a member.

Many bat species segregate sexes in the summer, forming sometimes large maternity and bachelor colonies at specific roost sites used year after year. This is especially true of females that care for and raise young in clustered settings. In natural areas, so-called nursery colonies congregate in rock crevices or shallow caves/mines that offer a proper thermal climate for that particular species. Larger colonies are susceptible to predation; therefore, most Rocky Mountain West species form smaller nursery groups of 20 to 100 individuals that can hide deep in rock crevices. Roost site temperatures in these crevices support ambient heat levels near normal body temperature, around 100°F (38°C), allowing females to sleep and not burn their own energy to keep a constant perfect temperature for gestation. However, some species, such as Townsend's big-eared bats (*Corynorhinus townsendii*), form nursery groupings composed of 20 to 40 individuals right out in the open in caves and abandoned mines, making them more susceptible to disturbance and predation (figure 1.18) (see Accounts of Species in chapter 6). At the other end of the spectrum, in tree-roosting bats, males and females are mostly solitary or form very small groupings of 2–3 individuals that commonly move from roost to roost.

Gestation periods in most Rocky Mountain West bats range between fifty and sixty days, after which the birth of a single youngster usually occurs. In the vast number of cases, females give birth to a single young; however, some tree species such as eastern red bats (*Lasiurus borealis*; figure 1.19) and tricolored bats (*Perimyotis subflavus*) may give birth to twins or even litters of four to five young (see Accounts of Species in chapter 6). Newborn young are typically between 25 and 40 percent of adult size at

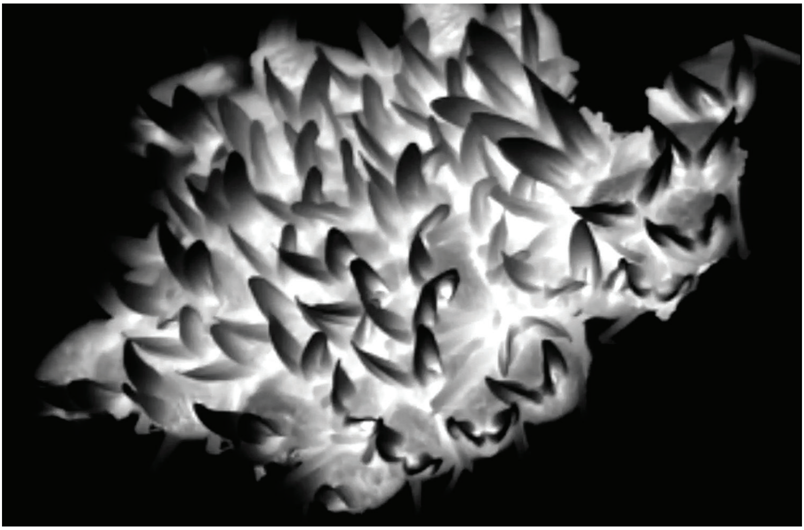

FIGURE 1.18. *Thermal image photograph of Townsend's big-eared bat (*Corynorhinus townsendii*) maternity colony roosting in Harmon Cave in Boulder County, Colorado (Will Keeley, with permission).*

birth. This would be equivalent to a 100-pound woman giving birth to a 20- to 40-pound child. This astonishing growth rate from a single-cell embryo occurs in just a couple of months. Even though large in body size, most young are born blind and hairless; they quickly climb onto their mother's chest and begin suckling fat-rich milk. From there, the amazing growth rate of the young continues, with them nearly adult size and beginning to fly in three–four weeks. This would be equivalent to a human newborn growing to adult size from birth in about six months. Females in nursery colonies share responsibility in caring for each others' young. When a mother leaves the roost to go feed, at least one female will remain behind and babysit until someone returns, releasing her for her turn to forage. Curiously, it has been observed that adult male big brown bats may also be present in the nursery colony, but whether these individuals have any role in rearing the young remains unknown. Once the young become volant (capable of flight), mothers take them out on foraging bouts to teach them the ropes. Mother and infant establish meet-up localities, such as trees, in case they get separated from each other. When netting bats during this time of year, it is not uncommon to catch mother and offspring simultaneously, indicating that they were flying together wing to wing.

FIGURE 1.19. *An eastern red bat (*Lasiurus borealis*) nursing three youngsters nearly her size (Merlin Tuttle, with permission).*

The Inner World of Bats: Emotions, Cognition, and Sentience

Humans have been slow to understand and accept the range and complexity of the socio-emotional lives of non-human animals. This is probably the most egregious and common type of human discrimination against other species (called speciesism) that persists today, and it occurs throughout all walks of life, cultures, and professions. Some scientists have begun to try to change this perspective, but human arrogance persists unchecked regarding unfounded inferiority biases toward other organisms. Humans have decided that our lives are more valuable and important than those of any other species on Earth and that torturing, killing, and slaughtering other animals is okay and justified, even simply for entertainment. But, of course, a mouse's or a bat's life means as much to them as our lives do to us. To think otherwise is illogical. The basic anthropocentric premise that human emotions, cognition, and sentience constitute some sort of pinnacle of evolution not achieved by other entities is not founded in any scientific studies, and, in fact, the opposite is verifiable. This baseless view, as a formal scientific perspective, dates back to writings by René Descartes (1596–1650), who insisted that non-human animals were not self-aware and lacked souls and minds. Indeed, Descartes wrote that non-human animals were no different than machines constructed by humans. This view not only made him, and other humans, feel superior but also absolved us of any moral responsibility toward other life forms. Science, as a general practice, considers other animals to be non-sentient, to lack emotions, and to not feel pain as humans do. Of course, there is no more scientific support for these ideas than for the perspective that other animals are very much the same as us. But in the field of science, the belief that non-human animals are capable of love and that they can be afraid, sad, or happy is considered anthropocentric and fundamentally unscientific. I find it interesting that all science works through probabilities that are based on the null hypothesis, which holds that there are no significant differences between entities unless they are shown to be statistically different. However, when it comes to animal thinking, intelligence, and emotions, suddenly this shifts to the alternative hypothesis that there is a significant difference unless statistically one can show that there is not.

The homocentric excuse for ignoring the socio-emotional lives of non-human animals has a long, disreputable history in science that is both unfounded and disappointing. Even the eminent primatologist Dr. Jane Goodall's work suffered for decades because other scientists bristled at the fact that she gave her chimp subjects names rather than simply numbers, thereby showing that she was biased and emotionally connected to the animals and that, therefore, her observations were at best inaccurate. Fortunately, Goodall did not give in to these ridiculous claims. Despite scientists still grappling with these medieval arguments, some researchers have broken away to design and implement research that allows insight into the cognitive and socio-emotional lives of non-human animals. As one might imagine, the more we look, the more profoundly the depths and breadths of other minds are revealed. Of course, anyone who lives with a pet rat, dog, cat, or crow can sense the wide arrays of personalities and behavioral quirks of these intelligent animals. Biology and wildlife departments at universities still teach students the ridiculous notion that only populations matter and the lives of individuals do not. In reality, as is our perspective regarding humans that all individuals matter, the same is true for non-human organisms, and there is no scientific justification for any other view. After all, it is individuals who carry mutations that may change the future survivability of populations and species; our ignorant and unwise random removal of them from populations could have significant conservation effects.

However, what makes the study of animal consciousness difficult is that there are no physical or genetic measures, per say, of consciousness because it is the outcome of interactions among complex biological systems. So, there is no structure we can call consciousness to measure and evaluate; rather, it is a state that appears de novo from interactions among the synapses of neurological tissue. Once the interactions stop, the phenomenon disappears. Furthermore, the physical entities that are interacting—in our example, the neurons—do not possess the emergent property that avails itself when they interact. For instance, a neuron is not likely conscious, but when many are put together and interactions form, consciousness is revealed. Thus, the properties of consciousness or intelligence are very difficult to quantify. Therefore, the question of whether all life is conscious, even down to single-cell organisms, has eluded scientists to this day.

Interestingly, later in his life, the father of the discovery of echolocation in bats turned his research focus to trying to understand animal consciousness, thinking, and emotions. He wrote two books on the subject titled *Animal Thinking* (1984) and *Animal Minds* (1992). Despite his notoriety and fame as a scientist, many colleagues immediately came out against his ideas and hypotheses, even though their arguments lacked any scientific validation. However, the idea of depth in the emotional lives of non-human animals is not new. Charles Darwin saw what others refused to see as early as 1872, when he authored a book titled *The Expression of the Emotions in Man and Animals*. In it, he compares facial expressions of non-human animals with their meanings if a human were expressing them. As an evolutionary biologist, Darwin saw animals' diverse minds as varying in degree, not in kind. In other words, the biochemistry of the brain is consistent and evokes similar manifestations among species, even though the reactions and specific interpretations to these stimuli may vary. Therefore, the expression (and thus the meanings) of emotions should be similar across groups, unless proven otherwise. However, testing this hypothesis is difficult and would require highly controlled and disciplined methods that remove human biases. As mentioned, this has begun to happen, and the discoveries are astounding in terms of the cognitive abilities of even the "simplest" organisms. Behaviors such as sociality and cooperation have deep evolutionary roots even in single-cell organisms that have no nervous systems, much less brains. Even plants have been shown to have information transfer systems and memories. This new frontier in biology will, it is hoped, change the way we interact with, and justify our behaviors imposed on, other organisms both as scientists and in our food and wildlife management philosophies.

As for bats, some innovative research is leading the way to changing our perspective on their socio-emotional lives. For example, well-designed research coming out of the Max Planck Institute in Germany as well as institutions in Switzerland has shown that bats have long-enduring, deep friendships that carry on for decades. In addition, bats have hierarchical relationships ranging from acquaintances to distant friends to close, more intimate relationships. These types of complex interactions place bats in the social status of other highly intelligent groups such as primates (including humans), dolphins and other cetaceans, and elephants; and we have only begun to skim the surface of the breadth and depth of bats' socio-emotional world. Neuroanatomist Dr. Jagmeet S. Kanwal, at Georgetown University in Washington, DC, has shown that baby bats babble similarly to human babies until they learn from their mothers how to construct information using proper syntax and diction. He has shown that bats are conscious, insightful, and highly malleable learners.

Bat Communities and Food Webs: The Tangled Bank

Darwin wrote in *The Origin of Species*: "It is interesting to contemplate a tangled bank, clothed with many plants of many kinds, with birds singing on the bushes, with various insects flitting about, and with worms crawling through the damp earth, and to reflect that these elaborately constructed forms, so different from each other, and dependent upon each other in so complex a manner, have all been produced by laws acting around us." More than 165 years later, we see biotic communities in much the same way but perhaps more formally. From microbes to bacteria to the multicellular forms, fundamentally, life is organized as assemblages of coexisting species that are intertwined in complex webs of interactions. These interactions also include nonliving (or abiotic) components of the environment that provide critical resources such as water, minerals, and the air we breathe.

It is important to keep in mind that humans are on the larger end of the scale of life forms. The average-size organism is unicellular, thus requiring a microscope to see; even many multicellular organisms are too small to see with the naked eye. Therefore, most interactions taking place in biotic communities are happening daily on a scale outside human perception, but simultaneously they are what support and allow life itself to persist in all its forms and activities. Furthermore, even within mammals, rodents, shrews, and bats compose 65 to 70 percent of all living forms. Most species are very small, weighing less than a quarter, and they go about their daily routine unnoticed by us. To emphasize this tiny world of great diversity and functional complexity beyond our immediate view, entomologist Edward O. Wilson elegantly expressed this point by stating that "a lifetime can be spent in a Magellanic voyage around the trunk of a single tree."

One way ecologists categorize interactions among organisms is in the form of food webs that seek to describe energy and nutrient flow across what are termed trophic levels. The first trophic level involves photosynthetic plants, referred to as autotrophs due to their ability to convert inorganic molecules (H_2O and CO_2) into organic ones (carbohydrates) that store energy to be used by themselves and other life forms. So, plants and other photosynthetic-capable microbes can make their own food, but all other organisms (called consumer heterotrophs) cannot; they rely directly or indirectly on autotrophs for survival. This process is also responsible for liberating oxygen that makes our atmosphere capable of supporting aerobic life forms. "Higher" trophic levels contain organisms that rely on predation. For vegetarians (primary consumers), this is called herbivory, and these organisms compose the second trophic level, with trophic level three (secondary consumers) those organisms that eat herbivores. Tertiary consumers involve those species that eat other carnivores. Energy captured by autotrophs travels to higher and higher trophic levels but declines precipitously, with only on average 10 percent of the previous level's energy transferred to the next (i.e., on average, 90% of energy captured by each trophic level is "lost"—released as heat) and unable to be captured by organisms feeding at the next higher level. Accordingly, as we move up the pyramid, the number of organisms that can be supported, as well as the number of individuals, is reduced by about 90 percent from the previous 10 percent transferred. For example, of 10,000 calories captured by autotrophs, only 1 calorie on average will make it to the tertiary trophic level. Insectivorous bats are living at the secondary consumer trophic level, whereas fruit bats are interacting at the primary consumer level, both of which have relatively high caloric values. Those bat species that consume vertebrates such as mice and birds or fish, blood, or other bats are tertiary consumers in which energy availability is low, thereby supporting fewer species.

However, bats may act across various trophic levels depending on their dietary complexity. In the Rocky Mountain West, nearly all species eat only insects, with a few nectar and pollen feeders. Curiously, once thought to be an obligate arthropod specialist, the pallid bat (*Antrozous pallidus*) has been observed visiting various species of blooming cactus for nectar (see Accounts of Species in chapter 6). So there are still surprises when it comes to the diets and trophic levels of specific bat species. Even a true pollinator and nectar-feeding specialist, such as the lesser long-nosed bat (*Leptonycteris yerbabuenae*), ingests insects that may be in the flowers it visits (see Accounts of Species in chapter 6).

But by and large, it seems that bats' most crowded trophic position is as a secondary consumer insectivore. This is not surprising because insects historically provide a huge and sometimes seemingly endless resource base. Unfortunately for bats, however, humans have reduced insect populations by at least 45 percent over the last few decades through the incessant use of pesticides, thereby threatening insectivorous bats and countless other species, including predatory insects and arachnids (e.g., spiders), amphibians, reptiles, birds, and mammals—all global food sources. Even more concerning, insect traps deployed over twenty-seven years in sixty-three nature-protected areas in Germany showed a 76 percent decline in flying insects, with a midsummer decline of 82 percent. Such losses have likely significantly disrupted the populations of bats, birds, and other species in those areas.

Although when we think of bats and insects we usually focus on predator-prey interactions, insects also act as ectoparasites on bats, including blood-sucking bat flies (Order: Diptera) and fleas (Siphonaptera), to name two commonly recognized groups. However, it is estimated that at least 687 insect species parasitize bats globally, along with various mites and ticks from the Class Arachnida (also including spiders, scorpions, and daddy longlegs). Indeed, bats' fur and skin is its own entire ecosystem, with complex interactions among coexisting ectoparasites.

Natural predators on bats are few. Smaller-bodied owls will hunt them down in night flight, and several species of hawks are known to infiltrate large groups of bats when they leave their roosts at night, grabbing as many as they can with their razor-sharp talons. Also, many bird species in the family Corvidae are highly carnivorous and will pull bats out of their roost sites in tree or rock cervices or even attack them if they are in flight before full darkness. Furthermore, snakes, some lizards, and many carnivorous or omnivorous mammals such as raccoons and wood rats will kill and eat bats if the opportunity presents itself.

Bats' influence in food webs goes much farther than the who-eats-who dimension of what we call niche space. Because many bat species use caves as well as cliff crevices that may ingress deeply into vertical rock faces, they act as conduits of energy and nutrient flow into underground and vertical subterranean areas where sunshine never pierces; therefore plants, which would provide primary production through photosynthesis, do not grow. In many cases, bats have formed large colonies in subterranean systems for many thousands of years. For example, two very difficult to access caves located in the Grand Canyon in Arizona, known as Double Bopper and Leandras Caves, were surveyed in 2022 and found to contain not only living colonies of bats but also thousands of dead bats. This allowed researchers to collect nearly 500 samples of mummified carcasses that could be identified to species. Then, through the use of radiocarbon dating, they were able to assess when these individuals died. They found that Townsend's big-eared bats (*Corynorhinus townsendii*) have occupied Double Bopper Cave continuously over the past 50,000 years (since the Upper Paleolithic, which covers the last glacial period [Stone Age] of human evolution); silver-haired bats (*Lasionycteris noctivagans*), which used both caves, have been present at least since the Holocene and Pleistocene Epochs—the last 11,700 years.

The long-term use of subterranean caverns of various types and dimensions, in some cases spanning millions of years, has supported unique and highly stable ecosystems wherein bat guano drives entire cave food webs that support hundreds or even thousands of species of arthropods, arachnids, and sometimes fish if water is present. In cases where bats have been exterminated from caves, entire underground ecosystems have collapsed. Although very little is known on the topic, bat guano appears to support cliff-face biodiversity by providing a nutrient base in rock crevices, both deep and shallow, that supports plant growth and arthropod diversity as well as predators such as lizards, snakes, and insect-eating shrews. In Jefferson County, Colorado, which has south-facing cliffs where bats commonly roost, thirteen unique and isolated plant species were found in these vertical ecosystems.

So, bats' effects in food webs stretch from streams to cliffs and into underground caverns that have been shown to house some of the most unique biodiversity on Earth. Certainly, other animals visit caves as well, but because bats form colonies that contain from hundreds to millions of individuals, deposition of their guano and urine can vastly increase the levels of

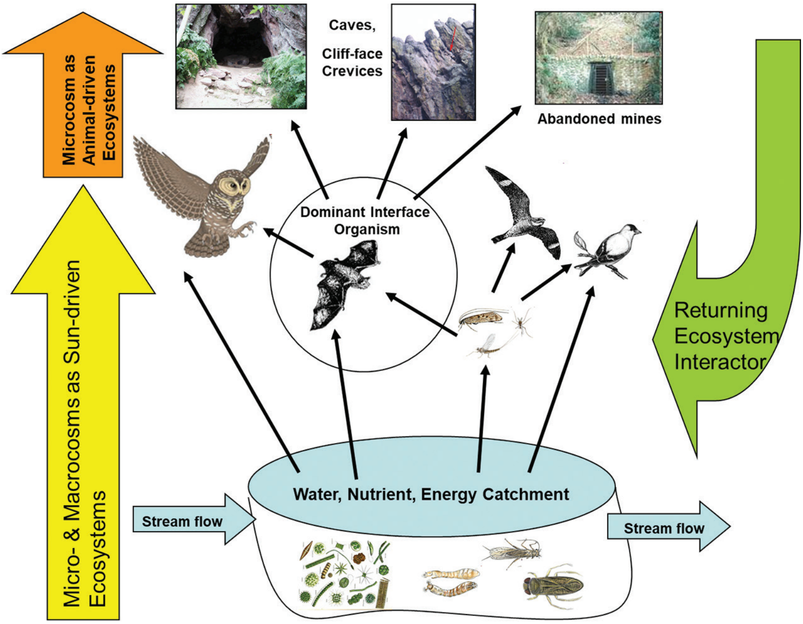

FIGURE 1.20. *Bats are novel interactors in food webs. Although bats act as both predator and prey in terrestrial ecosystems, uniquely, they also move energy, nutrients, and minerals into subterranean caves and mines as well as deep into rock crevices through the deposition of urine and guano. Many animals and plants thrive because of this; without bats, most subterranean ecosystems would not exist. The loss of bats has caused community collapses in these habitats.*

microbial, fungal, plant, and animal biodiversity even in deep caverns where sunlight does not penetrate (figure 1.20).

The Longer View: Aging in Bats

Another aspect that makes bats unique contributors to food webs and habitat health is their life span. Most small-bodied mammals live just a few years, whereas many bat species have been shown to have individuals that have lived for decades. Exact longevity for most bat species is unknown. However, what *is* known is unexpected and impressive. Most of the bats in the Rocky Mountain West are in the genus *Myotis* (family Vespertilionidae) and range in size from four to ten grams (between a nickel and a half dollar). However, some of these little bats can live longer than forty years. From an ecological standpoint, this means that colonies of bats, and their important contributions to ecosystem health, can be very stable for very long time periods. How bats accomplish such long lives on the order of what we see in bears and elephants remains a mystery, but some have hypothesized that during hibernation, metabolism is so slowed that this adds years to their life span. In hibernation, bats reduce their metabolic rate to about one heartbeat and one breath a minute, perhaps saving them significant physiological stress for nearly one third of each year.

However, medical research has shown that sections of DNA called longevity genes do exist and function to extend the average and maximum life span of many organisms, including humans. These genes are responsible for repairing DNA that is damaged through repeated replications. However, these genes can be overwhelmed by oxidative stress and thus fail to work, causing cells to malfunction and die. One's lifestyle can affect the function of longevity genes, as they are activated by calorie restriction, amino acid (protein) restriction, and adequately intense exercise. It has been shown that time spent being slightly too cold or too hot reduces oxidative stress on the body's cells and their DNA. Bats spend time at high body temperatures when they are flying, when their heart rate reaches 1,200 beats per minute. But many species also spend significant time at lower body temperatures when in torpor or hibernation (see chapter 3 for a more in-depth discussion of hibernation in bats). A recent study showed that in big brown bats (*Eptesicus fuscus*), longevity genes are related to those genes associated with hibernation, giving credence to the hypothesis that maintaining a body temperature just above freezing for extended periods may help increase their life spans. Corroborating this idea, rodent species that hibernate have about 15 percent longer life spans than those that do not. However, these rodents also have about half the number of offspring of non-hibernating rodents, and it has been shown that higher reproductive rates also reduce life spans in mammals. Thus, it is hard to tell if hibernation or reproductive rate is more important here. Curiously, although logically valid, the hibernation hypothesis has not been universally supported, as many tropical bats that do not hibernate have comparable life spans to those who do. However, all in all, on average, hibernating bats do live about six years longer than non-hibernating species.

Another cause of aging is the buildup of free radicals and oxidative stress that disrupts cellular function. Cells isolated from little brown bats (*M. lucifugus*) produced half to one-third the amount of hydrogen peroxide that causes oxidative stress per unit of oxygen compared to mitochondria from short-tailed shrews (*Blarina brevicauda*) and white-footed mice (*P. leucopus*), respectively. Furthermore, structures termed telomeres that function to protect DNA that typically shorten with age, thereby losing their function, did not shorten and remained fully active in bats in the genus *Myotis*, which seems to be key to their longevity. As is, for most bat species, we have no idea about life spans, but of the ones tested the range is rather wide (7–40+ years). Comparatively, if we look at our own taxonomic order, the Primates, life spans across about 500 species range from around two years in tarsiers to about forty years in chimpanzees and seventy-two years on average for humans. Within Chiroptera, which has more than 1,400 species, there is a similar but less broad range of life spans, and no known mammals of comparably small average body size and metabolism live nearly as long as bats. Uncovering the life span for most species of bats in the wild is difficult, as it requires somehow tracking them for what may be decades, so for most species we may never know. However, another process called methylenation of DNA has shown promise in providing a molecular ruler for aging that may be useful in assessing animal species' ages without having to track individuals over time.

The Global Importance of Bats

It is a human tendency to assign importance to other species based on their perceived value to human existence. Because of the long-standing practice of using animals for our own needs, many people have lost sight of the importance of all organisms in the function of ecosystems (yes, even mosquitoes are important). For example, we know that photosynthesis is the process by which plants take in carbon dioxide (CO_2) for its carbon and release the oxygen as a waste product of the reactions. However, just as most species do, plants also require oxygen for metabolism and growth. If you ask someone which organisms are most important for providing Earth's oxygen atmosphere, I think most would say trees/forests. Trees are big and therefore must be important in this process. Although trees and forests do their fair share of oxygen generation, they are also large and therefore must consume copious amounts. In reality, most atmospheric oxygen that supports life on Earth comes as a result of photosynthesis by oceanic plankton, single-cell organisms. So, although humans tend to give higher importance to larger organisms because, like us, they take up more space, in reality, it is the small organisms that underpin and drive our planet's ecosystems, thereby allowing the larger ones to exist at all.

As mammals go, bats tend to be on the smaller end of the spectrum and therefore tend to be dismissed as unimportant. Add to this that they are active at night, making their important activities shrouded from us, which has further resulted in human disregard. However, this has not stopped scientists from exploiting bats to help us better survive. The anticoagulant available in the saliva of common vampire bats (*Desmodus rotundus*) is used as an anti-clotting agent in human patients. Bat sonar has been the inspiration for developing similar artificial systems for humans suffering from blindness. Bats have even been used to help control mosquitoes and other insect populations and to reduce crop pests. Although in a human-centric worldview these contributions of bats to our endeavors may appear important, their importance to the rest of the natural world far exceeds our narrow-sighted values. Beyond humans, bats have immense importance in nearly every ecosystem worldwide.

In North America, bats are the only "serious" foragers of night-flying insects. Even though some birds—such as poorwills, nighthawks, and others in the goatsucker family—filter-feed insects from the night air, the impact of bats is magnified due to their larger and denser populations as well as excessively high metabolic rates. In fact, some bat colonies number in the millions of individuals, filtering tons of insects from the air every night. Although in most cases bats do not concentrate their foraging on one particular type of insect, an individual little brown myotis (*Myotis lucifugus*) has been shown to consume as many as 600 mosquitoes per hour under laboratory conditions and as many as 500 insects per hour in the wild. Multiplying this consumption rate by a colony containing several hundred "natural insecticides" quickly illustrates how bats affect insect populations. Colonies of Brazilian free-tailed bats (*Tadarida brasiliensis*), such as the one located in Colorado's San Luis Valley (figure 1.21), are estimated to consume almost a ton of insects nightly. But even this feeding frenzy pales in comparison to the consumption rate of huge colonies of *T. brasiliensis* in Texas, which ingest 150 tons of insects per night.

As they forage, bats consume a diversity of species such as moths, beetles, bees, mayflies, midges, flies, wasps, and surface-dwelling aquatic insects such as water boatmen. Many of the insects consumed by bats are known carriers of human and other animal diseases such as malaria, dengue fever,

FIGURE 1.21. *Exodus at dusk of more than 230,000 Mexican free-tailed bats (*Tadarida brasiliensis*) from the Orient Mine located in south-central Colorado's San Luis Valley. Mounds of accumulated guano drive a vast ecosystem inside the abandoned mine, which is a protected site today (author photo).*

and West Nile virus, as well as agricultural pests. Indeed, estimates in the United States alone show that insectivorous bats save farmers approximately $23 billion that they would otherwise incur annually in agricultural losses.

In tropical ecosystems, bats are fundamental to forest health, growth, and stability. Fruit-eating bats are responsible for dispersing more than 90 percent of the seeds of important plants such as figs (*Ficus*) that feed many other animal species. They are justly referred to as "farmers" of the forests because they disperse the seeds of their food plants, sometimes over tens of miles, sometimes in areas that have been deforested by humans. Each dispersal event includes a bit of guano that acts as fertilizer to encourage growth. Consumed seeds are partially digested when passed through the bat's stomach and intestines, and for some plants, this is a necessary first step in initiating seed germination. The essential role of bats in maintaining healthy tropical forests is unequivocal, and their importance in helping maintain global biodiversity is well founded. Indeed, studies have shown that in tropical areas where humans have clear-cut forests, plants that grow from bat-dispersed seeds initiate the process of forest regeneration. Clearly, bats are vital to this process.

In desert ecosystems, including those of the southwestern United States and Mexico, cross-pollination by bats is critical to successful reproduction of keystone plant species that support hundreds of other organisms in the harsh desert environments. For example, nectar-feeding bats such as the lesser long-nosed bat, *Leptonycteris yerbabuenae* (see Accounts of Species in chapter 6), cross-pollinate cardón, organ pipe, and saguaro cacti as well as agave and yucca plants (figure 1.22), all of which are keystone species of southwestern ecosystems. Unfortunately, long-nosed bats are currently endangered, and it is feared that extinction would precipitate a collapse of the desert ecosystems of the Southwest. In central Mexico, bats have been calculated to be worth US$2,500 per hectare (0.4 acres) for farmers on pitayas (*Stenocereus queretaroensis*) plantations who harvest the cactus fruits for market. In Brazil, bats save the country US$391 million annually due to their pest suppression ecosystem services.

The codependence between bats and their host plants illustrates what biologists term coevolution: complementary evolution between two or more species in a way that makes the fate of one reliant on the other or when involved species drive each other's evolution. The "arms race" between bats and insects described in the previous section is a type of coevolution because as either prey or predator gains an advantage, natural selection favors characteristics in the other that attempt to counter the advantage. Unlike predator-prey attempts to outfox each other observed in insectivorous bats, nectar-feeding bats and their host plants are driven by mutual benefits in behaviors and traits that further enhance and promote efficiency in the interactions (termed *mutualism*). For example, natural selection favors flower traits that enhance attractiveness to bats, such as increases in fragrance, visibility at night, and pollen transfer to the bat's fur. For bats, selection favors traits that allow for accessing nectar, such as greatly elongated tongues, the ability to hover in flight, and elongated snouts to reach deep into the base of the flower where nectar is stored. In this high-stakes Darwinian drama, those bats best suited for feeding at host plants will gain more energy for reproduction, and plants whose flowers attract more bats will also reproduce more than other plants. The individuals of both sides with the most efficient balance of give and take will be the most successful over generations in a timeless waltz that began eons before humans arose to hear the symphony. Thus, it is only in hindsight that we can marvel at its beauty and magnificence. As mentioned, this drama can be observed in the

FIGURE 1.22. *Lesser long-nosed bat (*Leptonycteris yerbabuenae*) visiting a saguaro cactus flower (M. Tuttle, with permission).*

southwest deserts of the Rocky Mountain West between columnar, saguaro, and organ pipe cactus and various species of long-nosed nectar-feeding bats.

Indeed, the magnificent bat fauna of the Rocky Mountains is highly diverse, and the interactions among bat species themselves as well as among many of the other living and nonliving ecosystem elements have produced a web of uniquely intertwined synergies and discordances. Even though nearly all bat species here are insectivorous, each employs emergent hunting techniques derived from particular suites of adaptive character states. Some species have wing shapes and echolocation frequencies adapted to open aerial foraging and they pursue their prey, sometimes at speeds approaching 50 mph, whereas others are adapted to dwell in forested stands that require slower flight speeds, allowing for maneuvering and navigating through vegetation while intercepting flying insects. Some have wings specialized to hover, listening for the sounds of fluttering moth wings on vegetation that cue them to approach and pick their prey directly from the surface of plants. Foregoing aerial foraging, some species such as pallid bats (*Antrozous pallidus*), present in desert areas throughout the Rocky Mountain West (see Accounts of Species in chapter 6), take to terrestrial pursuit of ground-dwelling beetles, grasshoppers, centipedes, and scorpions (figure 1.23).

FIGURE 1.23. *A pallid bat (*Antrozous pallidus*) taking off after pouncing on a giant desert centipede (*Scolopendra heros*) in Arizona. This bat species forages on the ground for scorpions, centipedes, and large beetles. It has also been known to feed occasionally on fruit and pollen (Merlin Tuttle, with permission).*

Alas, even blood-feeding bats known as vampire bats once navigated ecoscapes in the United States uncloaked by virtue of discovered fossils of an extinct relative of today's common vampire bats (*Desmodus rotundus*), found in several southern states. In 1968 a pregnant hairy-legged vampire bat (*Diphylla ecaudata*) was captured just twelve miles west of Comstock, Val Verde County, in Texas, significantly beyond this species' suspected northern range. It has also been suggested that with climate warming, vampire bats may again move northward into the United States.

An Unfortunate Loss of Biodiversity

Renowned evolutionary ecologist Eric R. Pianka once stated, "Once we were surrounded by wilderness and wild animals, but now, alas, we surround them" (2006: n.p.). We are currently witnessing the sixth mass extinction of life on Earth. The first five varied in intensity, wiping out anywhere from 50 to 96 percent of Earth's species. The fifth mass extinction, often referred to as the Cretaceous extinction, occurred 65 MYA and is probably the best known because it included the dinosaurs. However, it wiped out 76 percent of all life forms, not just the biggest lumbering ones. Mammals capitalized on this extinction event by coming to dominate the planet after spending 100 million years in the shadows of giants like *Tyrannosaurus rex*. As mentioned, full-bodied bat fossils trace to about 55 MYA, so these flying mammals were present shortly after this extinction event.

Although these mass extinction events are important evolutionary processes that "reset" planetary boundaries for life, the sixth mass extinction currently in play is happening an estimated 1,000 times faster than any of the others and is being caused, for the first time ever, by a single species' overconsumption of resources and destruction of natural habitats that support the other 10 million species with which humans share the Earth. Bats are no exception in feeling humanity's devastating effects on global environments. Despite perhaps as many as 65 million years of success, many bat populations are in serious decline. The International Union for the Conservation of Nature (IUCN) estimated that minimally, 21 species are critically endangered (face imminent extinction risk), 83 are endangered, 109 are considered vulnerable, and 242 are "data deficient," indicating concern for their survival. Of the 45 bat species in North America, more than 30 percent qualify as vulnerable, imperiled, or critically imperiled (NatureServe NGO, https://www.natureserve.org/). In addition, because most bat populations are so difficult to track, it is impossible to assess the current condition of many species. This is particularly true in the Rocky Mountain West, where the terrain is rugged and expansive. In a global sense, although bats enjoy high species diversity, which to the casual observer may suggest ecological stability, the order Chiroptera is in crisis due to apparent large-scale regional losses of populations of numerous species.

Reasons for declines in bat populations are abundant, but habitat loss over the past two centuries is one prime suspect. For example, logging practices have caused a 99 percent decline of virgin forests in the United States (figure 1.24), decimating populations of animal species—including bats—that relied on them for survival. In addition, bat populations have been subjected to heavy pesticide contamination, seriously affecting reproduction and survivorship. In particular, the use of DDT in the 1950s and 1960s is thought to be responsible for more than a 90 percent decline (from 4 million to fewer than 200,000) of Brazilian free-tailed bats (*Tadarida brasiliensis*) at Carlsbad Caverns, New Mexico. I will come back to the many causes of bat declines in chapter 5.

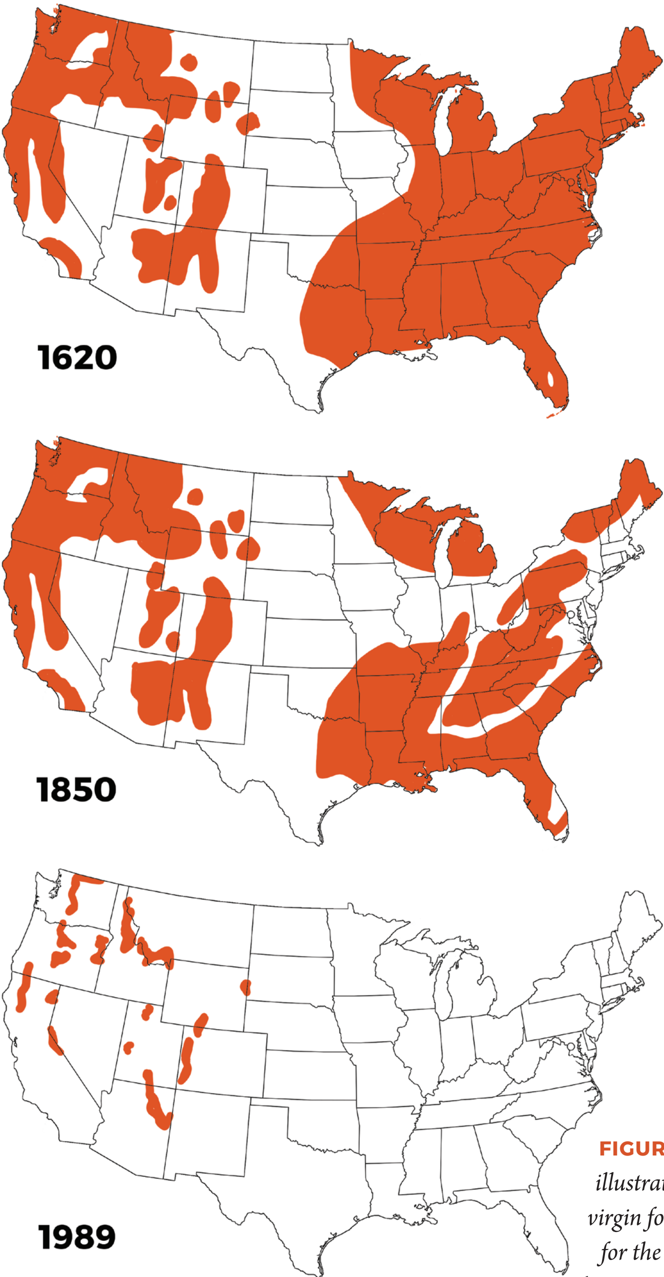

FIGURE 1.24. *Maps illustrating the loss of virgin forest estimated for the United States between 1620 and 1989 (United States Forest Service, public domain).*