

Chapter 15

Recent Advances in Bat Migration Research

Jennifer J. Krauel and Gary F. McCracken

Abstract In this chapter we discuss the state of research on bat migration and compare some of these patterns to those of birds. We begin with an overview of the literature on migration, apply migration theory, and discuss case studies on four bat species on which the greatest knowledge and understanding of migratory patterns exists. We also discuss what is known of motivating factors for bat migration and where research needs are apparent.

15.1 About Migration

Migration is the movement of animals that are following seasonal availability of resources and strategies involve an astonishing variety of schemes. Birds and mammals differ from insects in migration: individual birds and mammals can do many round trips, usually reproducing only once per trip (but see Rohwer et al. 2009), whereas insects typically undergo multiple generations per migratory cycle (Drake and Gatehouse 1995). Dingle (1996) asserted that migrating animals display some or all of the following characteristics: (1) traveling longer distances and in relatively straighter lines than during foraging, (2) displaying special predeparture or post-arrival behaviors such as hyperphagia, (3) storing energy to use during or after the trip, and (4) not displaying normal responses to stimuli such as pheromones or prey. Migration differs from dispersal which is generally unidirectional.

Understanding animal migration is important. Migratory animals include wild birds that span political borders and spread zoonotic disease that can affect humans

J.J. Krauel (✉) • G.F. McCracken
Department of Ecology and Evolutionary Biology,
University of Tennessee, 569 Dabney Hall, Knoxville, TN 37996, USA
e-mail: jkrauel@utk.edu; gmccrack@utk.edu

(see Chap. 16) and agricultural insect pests such as the corn earworm (*Helicoverpa zea*) which cause billions of dollars of economic damage. Migratory bats help suppress migratory pests (Lee and McCracken 2005). The migratory lesser long-nosed bat (*Leptonycteris curasoae*, Fleming 2004) and the straw-colored fruit bat (*Eidolon helvum*, Richter and Cumming 2008) are important pollinators and seed dispersers following seasonal blooms of flowers and fruit over thousands of kilometers and international borders. Moving animals transfer energy and nutrients among ecosystems (Wikelski et al. 2007). Migratory animals also face habitat fragmentation and climate change, which are likely to be disruptive (Sherwin et al. 2012; Wilcove and Wikelski 2008). In addition, increasing deployment of wind turbines to counter climate change kills thousands of migratory, and other, bats (see Chap. 20).

15.2 Overview of Migration in Bats

There are several reviews on bat migration (Cryan and Veilleux 2007; Fenton and Thomas 1985; Fleming and Eby 2003; Griffin 1970; Hutterer et al. 2005; Popa-Lisseanu and Voigt 2009) showing at least 87 species in 10 families for which all or part of a population migrates regionally or longer-distance (Table 15.1). Most migration research concerns birds (Faaborg et al. 2010) that have some similarity with bats (Dingle 1996), but there are significant differences in scale and behavior. Bat migration is much less common than in birds (Brigham et al. 2012; Woods and Brigham 2004), covers shorter distances and possibly shorter stopover intervals (Fleming and Eby 2003), and involves foraging while migrating.

Bats migrate to follow roosts and/or food (Fleming and Eby 2003). In temperate areas, some bats move regionally (100–500 km each way) to and from hibernacula (Rodrigues and Palmeirim 2008). Long-distance (~>1,000 km) migrants in temperate areas often forgo hibernation by overwintering in milder climates offering food (Fleming and Eby 2003), although some European bats undergo long migrations to hibernacula (Hutterer et al. 2005). In tropical or subtropical areas, long-distance migrants follow transient fruit or nectar resources (Fleming and Eby 2003). Whether insect-eating bats migrate in response to seasonally available prey remains unknown as these patterns are obscured by the lack of information on seasonal insect availability beyond agricultural pests. Although regional migrants are assumed to move in search of roost sites (Griffin 1945, 1970; Tuttle 1976), many latitudinal migrants may be pursuing food, with roosts being a secondary factor.

Migratory behavior appears to have independent, multiple evolutions, especially in the western hemisphere (Bisson et al. 2009; Popa-Lisseanu and Voigt 2009). The origin of most bat species and the greatest diversity occurs in the tropics where more stable resource bases occur; thus, temperate species migration is not likely an ancestral trait (Fleming and Eby 2003). Although migratory behaviors in bats are probably less diverse than in birds, some patterns exist. For example, there is sex-based migration (Ibanez et al. 2009), with females moving farther north in the spring in North America (Cryan 2003, but see Kurta 2010) as well as in Europe and Australia

Table 15.1 Bats known to migrate or suspected of migration with longest documented one-way migration distance (km)

Family	Species if known	Distance	References
Molossidae	<i>Eumops perotis</i>		Medellin (2003)
	<i>Eumops underwoodi</i>		Medellin (2003)
	<i>Mops condylurus</i>		McGuire and Ratcliffe (2011)
	<i>Nyctinomops macrotus</i>	L	Medellin (2003)
	<i>Otomops madagascariensis</i>		CMS (2012)
	<i>Otomops martiensseni</i>		CMS (2012)
	<i>Tadarida brasiliensis</i>	1,800	Cockrum (1969)
	<i>Tadarida insignis</i>		Funakoshi and Yamamoto (2001)
	<i>Tadarida latouchei</i>		CMS (2012)
	<i>Tadarida condylura</i>		O'Shea and Vaughan (1980)
	<i>Tadarida bemmellini</i>		O'Shea and Vaughan (1980)
	<i>Tadarida punila</i>		O'Shea and Vaughan (1980)
	<i>Platymops setiger</i>		O'Shea and Vaughan (1980)
Phyllostomatidae	<i>Anoura geoffroyi</i>		Medellin (2003)
	<i>Carollia perspicillata</i>	<200	Fleming (1988)
	<i>Choeronycteris mexicana</i>	L	Valiente-Banuet et al. (1996)
	<i>Leptonycteris curasoae</i>	>1,000	Cockrum (1991)
	<i>Leptonycteris nivalis</i>	>1,000	Moreno-Valdez et al. (2004)
	<i>Leptonycteris sanborni</i>		Cockrum (1991)
	<i>Platalina genovensium</i>		CMS (2012)
	<i>Sturnira lilium</i>		Mello et al. (2008)
Vespertilionidae	<i>Antrozous pallidus</i>	R	Medellin (2003)
	<i>Barbastella barbastellus</i>	290	Hutterer et al. (2005)
	<i>Eptesicus fuscus</i>		Medellin (2003)
	<i>Eptesicus nilssonii</i>	450	Hutterer et al. (2005)
	<i>Eptesicus serotinus</i>	330	Hutterer et al. (2005)
	<i>Ia io</i>		McGuire and Ratcliffe (2011)
	<i>Lasionycteris noctivagans</i>	U	Cryan (2003)
	<i>Lasiurus borealis/blossevillii</i>	U	Cryan (2003)
	<i>Lasiurus cinereus</i>	U	Cryan (2003)
	<i>Lasiurus ega</i>		Medellin (2003)
	<i>Lasiurus intermedius</i>		Medellin (2003)
	<i>Lasiurus seminolus</i>	U	Perry et al. (2010)
	<i>Lasiurus xanthinus</i>		Medellin (2003)
	<i>Myotis auriculus</i>		Medellin (2003)
	<i>Myotis blythii</i>	488	Hutterer et al. (2005)
	<i>Myotis brandtii</i>	618	Hutterer et al. (2005)
	<i>Myotis californicus</i>		Medellin (2003)
	<i>Myotis capaccinii</i>	140	Hutterer et al. (2005)
	<i>Myotis chiloensis</i>		Fleming and Eby (2003)
	<i>Myotis ciliolabrum</i>		Medellin (2003)
<i>Myotis dasycneme</i>	350	Hutterer et al. (2005)	
<i>Myotis daubentonii</i>	304	Hutterer et al. (2005)	
<i>Myotis evotis</i>		Medellin (2003)	

(continued)

Table 15.1 (continued)

Family	Species if known	Distance	References
	<i>Myotis griescens</i>	>500	Tuttle (1976)
	<i>Myotis lucifugus</i>	>500	Fleming and Eby (2003)
	<i>Myotis myotis</i>	436	Hutterer et al. (2005)
	<i>Myotis mystacinus</i>	240	Hutterer et al. (2005)
	<i>Myotis nattereri</i>	327	Hutterer et al. (2005)
	<i>Myotis sodalis</i>	500	Fleming and Eby (2003)
	<i>Myotis thysanodes</i>		Medellin (2003)
	<i>Myotis tricolor</i>		O'Shea and Vaughan (1980)
	<i>Myotis velifer</i>		Medellin (2003)
	<i>Myotis volans</i>		Medellin (2003)
	<i>Myotis yumanensis</i>		Medellin (2003)
	<i>Nyctalus lasiopterus</i>	U	Hutterer et al. (2005)
	<i>Nyctalus leiseri</i>	1,568	Hutterer et al. (2005)
	<i>Nyctalus noctula</i>	1,546	Hutterer et al. (2005)
	<i>Perimyotis subflavus</i>	R	Fleming and Eby (2003)
	<i>Pipistrellus nathusii</i>	1,905	Hutterer et al. (2005)
	<i>Pipistrellus pygmaeus</i>	U	Hutterer et al. (2005)
	<i>Pipistrellus pipistrellus</i>	1,123	Hutterer et al. (2005)
	<i>Scotoecus hindei</i>		O'Shea and Vaughan (1980)
	<i>Scotophilus nigrita</i>		O'Shea and Vaughan (1980)
	<i>Vespertilio murinus</i>	1,787	Hutterer et al. (2005)
Miniopteridae	<i>Miniopterus australis</i>		McGuire and Ratcliffe (2011)
	<i>Miniopterus inflatus</i>		McGuire and Ratcliffe (2011)
	<i>Miniopterus natalensis</i>		Miller-Butterworth et al. (2003)
	<i>Miniopterus schreibersi</i>	833	Hutterer et al. (2005)
Emballonuridae	<i>Emballonura monticola</i>		CMS (2012)
	<i>Emballonura semicaudata</i>		CMS (2012)
	<i>Taphozous mauritianus</i>		O'Shea and Vaughan (1980)
	<i>Taphozous melanopogon</i>	200	Gopalakrishna (1986)
Pteropodidae	<i>Eidolon helvum</i>	1,500	Thomas (1983)
	<i>Epomorphorus wahlbergi</i>		McGuire and Ratcliffe (2011)
	<i>Myonycteris torquata</i>	750	Thomas (1983)
	<i>Nanonycteris veldkampii</i>	750	Thomas (1983)
	<i>Pteropus alecto</i>	U	Breed et al. (2010)
	<i>Pteropus poliocephalus</i>	978	Ratcliffe (1932)
	<i>Pteropus scapulatus</i>		Ratcliffe (1932)
	<i>Pteropus vampyrus</i>		Epstein et al. (2009)
Hipposideridae	<i>Hipposideros commersoni</i>		O'Shea and Vaughan (1980)
	<i>Hipposideros lankadiva</i>	475	Gopalakrishna (1986)
	<i>Triaenops persicus</i>		O'Shea and Vaughan (1980)
Rhinolophidae	<i>Rhinolophus landeri</i>		O'Shea and Vaughan (1980)
	<i>Rhinolophus hildebrandti</i>		CMS (2012)
Megadermatidae	<i>Cardioderma cor</i>		O'Shea and Vaughan (1980)
Rhinopomatidae	<i>Rhinopoma microphyllum</i>	900	Gopalakrishna (1986)

L long-distance migrant, *R* regional migrant, *U* maximum distance unknown, blank indicates no distance information available

(Fleming and Eby 2003). Bats also migrate in groups, sometimes even mixed-species groups (Cryan and Veilleux 2007; Fleming and Eby 2003). Bat migration sometimes coincides with mating behavior (Cryan and Veilleux 2007). Migratory bats typically share similar morphologies like high wing aspect ratios and high wing loading (Norberg and Rayner 1987) facilitating high-speed, long-distance flight. However, behavioral and morphological characteristics likely facilitated the evolution of migration, rather than being a causal agent (Fleming and Eby 2003).

Bisson et al. (2009) suggest that migration evolved independently in several vespertilionid lineages. Many cave-roosting *Myotis* are regional migrants but none move long distances. In contrast, many species of *Lasiurus* are long-distance migrants, but none appear to be regional migrants. Thus, Bisson et al. (2009) conclude that long-distance migration is less likely to have evolved in cave- than in tree-roosting bats, in contrast to how migration evolved in birds, starting with short- to long-distance migrations. However, Berthold (1999) posits that the evolution of migration in birds is ancestral and likely driven by coexistence of both migratory and nonmigratory genes in the same population, expressed depending on a threshold variable. Thus, ecology, morphology, or perhaps physiology drives the evolution of migration, and this could explain the probable independent evolution in multiple lineages of bats.

Tracking bats during seasonal movements is especially difficult, and what we know comes from large-scale banding efforts conducted in the first half of the twentieth century (Cockrum 1969; Glass 1982; Griffin 1945; Hutterer et al. 2005; Steffens et al. 2007; Tuttle 1976) wherein more than a million bats in Europe and North America were captured at roosts and banded, with recovered bands showing clues to seasonal movements. Individual Brazilian free-tailed bats (*Tadarida brasiliensis*) banded in caves in southwestern USA show some individuals moved 1,800 km into Mexico, at rates of about 50 km/day (Cockrum 1969; Glass 1982). In Europe, banding started in the 1940s in seven countries and continues today in 35 countries. Data are available for 47 European species of bats and consolidation of records is underway, but even partial results show a striking pattern of movement for many long-distance migrants between northeastern and southwestern Europe (Hutterer et al. 2005). Banding of bats in North America and several European countries has decreased after massive banding-related mortality, often associated with inexperienced banders (Ellison 2008, but see Rodrigues and Palmeirim 2008). Although banding can be harmful to bats, tracking individual bats is crucial to understanding bat migration, and improvements in banding technology would greatly assist in this effort.

15.3 Applying Migration Theory to Bats

There is considerable theoretical and integrative research on migration (Berthold 1999; Dingle 2006), but almost all treatments ignore bats (e.g., Akesson and Hedenstrom 2007; Chapman et al. 2011; Dingle 2006; Hein et al. 2012, but see Hedenstrom 2009) because knowledge remains patchy and often information such

as which species migrate, population sizes of those species, and their migratory routes remains unknown. Although population sizes of North American migratory tree bats are considered not measurable (Carter et al. 2003), we cannot clearly estimate the magnitude of any threat without population estimates. Applications of molecular data offer estimates of current and historical population sizes and should be explored (Russell et al. 2011). Also, current tracking technology is limited (Holland and Wikelski 2009). Thus, fundamental research must still be addressed before migration theory can be applied to bats.

Migration appears to be a plastic behavior. In birds, substantial genetic variation for migration propensity, distance, and direction exists even in partial or nonmigratory populations (Pulido 2007, 2011), and many bird species change their migration patterns or stop migration altogether (Sutherland 1998). For example, house finches (*Carpodacus mexicanus*) introduced to eastern North America from a nonmigratory population quickly adopted migration (Able and Belthoff 1998). Populations of blackcaps (*Sylvia atricapilla*) that previously migrated from Europe to the Mediterranean and Africa now overwinter in the British Isles (Pulido 2007). Partial migration, where migrant and nonmigrant conspecifics share a common site during one period of their annual cycle, is common (Chapman et al. 2011; Berthold 1999). Many bat species are partial migrants (Fleming and Eby 2003). In some species (North American tree bats), males and females appear to migrate differently (Cryan 2003), and in others (e.g., Brazilian free-tailed bats), only part of the population migrates (Laval 1973). Moussy et al. (2012) review the effect of migration and dispersal on genetic structure of populations.

Migratory birds have smaller brains than nonmigrants (Sol et al. 2005). McGuire and Ratcliffe (2011) show a similar pattern with bats and suggest that transporting smaller, less massive brains supports an energy trade-off hypothesis. Alternatively, larger brains in nonmigrants may reflect selection for behavioral flexibility and the need to find food in seasonally variable habitats and this might also explain why migratory birds are less successful invaders (Sol and Lefebvre 2000). Although brain size is smaller, the hippocampus, important to spatial memory in many birds and mammals (Moser 2011), is proportionately larger in migratory birds, but not in migratory bats (McGuire and Ratcliffe 2011). Avoiding seasonal variation in resources by hibernating may result in less selection for behavioral flexibility in nonmigratory bats.

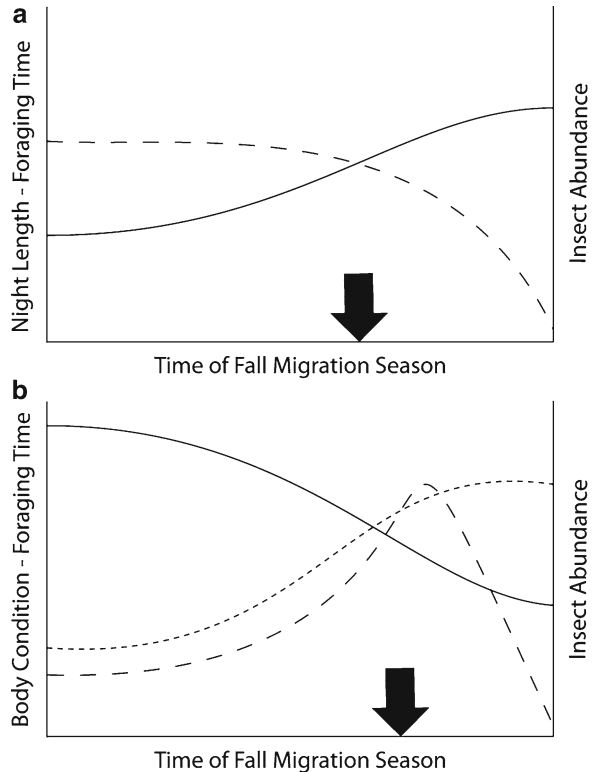
Most birds fuel their migration primarily through fat stores (Gwinner 1990) as do many bats (McGuire et al. 2009), and the processes of acquiring and using fat stores, both for migration and hibernation, are a focus of current research. In many mammals increased fat increases leptin production, resulting in appetite inhibition and increased metabolic rate (Florant and Healy 2012). In little brown bats, body mass increased before migration and hibernation, but leptin levels were low and even dissociated with fat deposition (Kronfeld-Schor et al. 2000; Townsend et al. 2008) which might explain the ability of bats to continue adding fat. Decreased adiponectin has been linked to obesity in rodents; however, adiponectin levels decreased in tissues of fattening bats but not in circulation, indicating that seasonal weight gains in bats differ from pathological weight gain (Townsend et al. 2008).

That bats use stored fat for migration has been suggested (Fleming and Eby 2003; O'Shea 1976; Tuttle 1976), but it is difficult to distinguish between fat used for migration as opposed to hibernation (McGuire and Guglielmo 2009), and these two uses may be fundamentally different. Most mammals fuel high-intensity exercise primarily through protein and carbohydrates, and the ability to use stored fat for extended migration is not well documented (McGuire and Guglielmo 2009). When actively foraging, bats use energy from harvested insects rather than stored fat (Voigt et al. 2010), and there is growing evidence that bats forage while migrating (Reimer et al. 2010; Valdez and Cryan 2009). A study of fat storage in hoary bats (*Lasiurus cinereus*), not known to hibernate, found differences in body fat percentage in those captured during migration versus nonmigration periods and increased enzymes indicative of stored fat conversion during migration (McGuire et al. 2013). Further, females had larger fat stores and optimized intercellular fatty acid transport structures which may be related to spring migration during pregnancy (McGuire et al. 2013). Pregnant female hoary bats are less likely than males to use torpor (Cryan and Wolf 2003) and travel greater distances than males (Cryan 2003). McGuire et al. (2013) also reported lower body weights in migrating than nonmigrating hoary bats as well as reduced size of digestive organs, thereby reducing the weight carried during migration. Reduced digestive organs suggest that foraging during migration is opportunistic rather than required. The combination of increased fat reserves and the use of daily torpor distinguishes bat and bird migration strategies. Foraging by bats may act to "top off" fuel reserves, whereas birds "empty their tanks" and completely refuel during migratory stopovers (McGuire 2012). Another intriguing difference is an increase in lung capacity in bats during migration, not observed in birds (McGuire et al. 2013).

The time available for feeding is the main limiting factor in bird migration distance (Kvist and Lindstrom 2000), resulting in a metabolic ceiling for storing fat despite the ability of passerine birds to migrate at night and feed by day. Hedenstrom (2009) using a migratory model showed that because most bats neither feed nor migrate diurnally, time and fueling are more constrained in bats than birds. He proposed selection pressure between autumn's longer nights for feeding and transport and lower food abundance as winter approaches, resulting in an optimal migration period (Fig. 15.1a). This model assumes that bats do not forage during migration, which may be invalid. In addition, bats generally do not spend entire nights foraging (Shiel et al. 1999). For example, length of night was not related to foraging time for female hoary bats, even after parturition when energy needs were high (Barclay 1989). Finally, Hedenstrom (2009) did not consider the fluctuating availability of migratory insects, an important influence on an optimal migration date (Lee and McCracken 2005; Rydell et al. 2010). We present an alternate model (Fig. 15.1b) using fluxes in insect availability and corresponding changes in foraging times; some level of body condition (mass or lipid levels) would predict optimum departure time.

Birds and other animals use a variety of sensory cues in orientation and navigation (Akesson and Hedenstrom 2007) and often adhere to map and compass theory, i.e., determining position with respect to the goal (map) and determining goal

Fig. 15.1 (a), after Hedenstrom (2009), the *solid line* represents night length (available foraging time) as a surrogate for body condition. *Dashed line* denotes insect abundance; *arrow* indicates optimal time for maximum migration speed; (b) represents an alternative model where insect abundance is lower and rises with fluxes of migrating insects. Line designations as in (a). Departure time to permit optimum migration speed is a function of body condition is represented by the dotted line in (b), which tracks insect abundance



direction (compass). Map theory has been applied to adult avian migrants, reptiles, amphibians, and fish, and compass orientation is common in arthropods and juvenile birds (Holland 2007). Bats have good spatial memory (Holland et al. 2005) and Tsoar et al. (2011) showed that Egyptian fruit bats (*Rousettus aegyptiacus*) use multiple visual landmarks for navigation, but long-distance homing involves other mechanisms. Like many animals, bats can sense Earth's magnetic field (Holland et al. 2006) which can provide two types of directional information: inclination (direction toward or away from the equator) and polarity (north/south direction). Birds are thought to respond only to inclination (Beason 2005). The preference of the Chinese noctule (*Nyctalus plancyi*) to roost in the north end of their cage suggested a response to magnetic polarity (Wang et al. 2007). Bats calibrate the magnetic field using sunset (Holland et al. 2008) but unlike birds, do not appear to use polarized light for calibration (Holland et al. 2010). Bats that emerged long after sunset did not use a star compass calibrated by the geomagnetic field in place of sunset calibration (Holland et al. 2010) and thus responded differently than birds.

Many animals migrate using specific routes (Dingle 1996) and so apparently do bats. Lesser long-nosed bats follow a specific and relatively narrow path through a resource gradient (Fleming 2004; Morales-Garza et al. 2007), but most migration routes are probably broader and more diffuse. Tree bats in North America follow

regular routes and are netted in specific locations at specific times, but these observations are anecdotal (Cryan and Veilleux 2007; Valdez and Cryan 2009). Tree bats appear to track closer to roost sites along mountain ranges (Baerwald and Barclay 2009) and avoid crossing open prairies. Other insectivorous bats follow linear landscape features to specific departure points before crossing open ocean (Ahlen et al. 2009), and it is not uncommon for migrating bats to follow riparian zones and shorelines (Barclay 1984; Serra-Cobo et al. 1998; Furmankiewicz and Kucharska 2009).

Many migratory birds use stopover sites (Berthold and Terrill 1991; Hedenstrom 2008), and there is evidence for this in bats (Cryan and Brown 2007; Dzal et al. 2009; Taylor et al. 2011), but if they remain for extended periods or are simply foraging along the way remains generally unknown. The definition of a migratory stopover is scale- and species-specific (Taylor et al. 2011). Cryan and Brown (2007) reviewed records of hoary bats “stopping over” on the Farallon islands during fall migration and found them present for 1–35 days during the fall, but could not quantify how long any individual stayed. Silver-haired bats *Lasionycteris noctivagans* stopped for several days during spring migration at a lake in Manitoba, Canada (Barclay et al. 1988). Dzal et al. (2009) found evidence that silver-haired bats and hoary bats use Long Point, Ontario, Canada, as a migration flyway, and that *L. noctivagans* stopped over during August. Taylor et al. (2011) and McGuire et al. (2011) radiotracked 30 *L. noctivagans* at Long Point in fall 2009 and observed seven “stopover flights” and 23 distinct migratory departures. However, most stayed only one night except when weather conditions forced delay, and most had sufficient fat reserves to complete migration without additional foraging (McGuire et al. 2011). *Myotis lucifugus* are the most common species at Long Point, and Dzal et al. (2009) found that the genetic diversity during fall migration was higher than at swarming areas, suggesting that bats assemble there from diverse areas before crossing the lake. In Texas, *Tadarida brasiliensis* show a fall, and to a lesser extent spring, spike in their use of urban roosts, indicating possible migration stopovers (Scales and Wilkins 2007). Populations of *T. brasiliensis* vary at Carlsbad Cave, New Mexico, including a large temporary increase in mid-October (Altenbach et al. 1979; Hristov et al. 2010). Cockrum (1969) anecdotally reports hundreds of thousands of these bats arriving overnight at caves during migration and then departing days later, consistent with our own observations in fall at Frio Cave, Texas. Many of these caves apparently function as maternity roosts as well as migratory stopovers.

Weather influences migration for most flying animals (Shamoun-Baranes et al. 2010) including birds (Able 1973; Liechti 2006; Nisbet and Drury 1968). Most nocturnal migrant birds fly in tailwinds or light winds rather than strong or headwinds (Richardson 1990). Migratory bats are also more active in light winds (Arnett et al. 2008; Horn et al. 2008). Hoary bats were more likely to land on an island stopover during low wind periods, low moon illumination, higher cloud cover, and to a lesser extent low barometric pressure (Cryan and Brown 2007). However, a separate study documented this species flying often in unfavorable winds (Baerwald and Barclay 2011). Silver-haired bats were less likely to leave a stopover and continue migration during rain (McGuire et al. 2011). The timing of bird migration is related to cold fronts, especially during strong cold fronts in North America with falling pressure and temperature (Able 1973; Richardson 1990). Bats also migrate

with cold fronts (Cryan and Brown 2007). Birds with high wing loading and aspect ratio are less affected by weather variables during spring migration (Saino et al. 2010) as presumably should bats having similar wing form. Migratory insects normally fly at much slower speeds than birds and bats, but during migration insects achieve similar speeds by moving with favorable wind conditions (Alerstam et al. 2011). There is evidence that bats take advantage of concurrent migration patterns to forage on migrating insects (Lee and McCracken 2005) and even birds (Ibanez et al. 2001; Popa-Lisseanu et al. 2007).

15.4 Four Examples of Bat Migration

Baker (1978) distinguished between facultative and obligate migrants. Facultative migrants are sensitive to local cues like resource availability and may not migrate without them. Obligate migrants are less sensitive to cues and most individuals migrate even if resources remain locally available. The hoary bat is an example of a tree-roosting long-distance migrant, with a primarily north–south migration route, is not known to hibernate, and is a likely obligate migrants. The second example, Schreiber’s bent-winged bats, is another probable obligate migrant and an example of regional migrants that move seasonally between maternity and hibernacula caves. These widespread old-world bats do not appear negatively affected by banding (Rodrigues and Palmeirim 2008), and we summarize information connecting behavior, population structure, and movement. Third, Brazilian free-tailed bats are facultative migrants with North American populations that vary widely in migratory behavior, distance, sexual bias, and direction. Finally, we include here a long-distance tropical migrator, straw-colored fruit bat and compare its migration to long-distance movements of other tropical fruit bats.

15.4.1 Long-Distance Migrant Tree Bats: Hoary Bats

A sense of urgency for research on long-distance migration by tree-roosting bats is motivated due to the large numbers of these bats killed by wind turbines (see Chap. 20).

In the spring, female hoary bats move through New Mexico about a month earlier than males, and they apparently travel in groups, fly below the canopy along streams, and forage during migration (Valdez and Cryan 2009). Females are usually pregnant during spring migration and less likely to use torpor (Cryan and Wolf 2003). Both in spring (Valdez and Cryan 2009) and fall (Reimer et al. 2010), the diet of hoary bats consists primarily of moths. Based on carcasses found at wind energy facilities, male hoary bats passed through Alberta, Canada, in late July, followed by females and young in early mid-August (Baerwald and Barclay 2011), and in the fall, hoary bats were recorded more often by acoustic detectors set at 30 m, than at or 67 m above ground level (Baerwald and Barclay 2011). Hoary bats may fly at higher altitudes in fall than in spring (Johnson et al. 2011; Valdez and Cryan 2009),

although it is possible that bats are flying too high for detection in spring. At the Canadian wind facility, hoary bat activity was best predicted by falling barometric pressure, and this was reflected in fatality rates (Baerwald and Barclay 2011).

A comparison of acoustic detection sites on a north/south gradient across the Eastern USA reveals a pattern of hoary and silver-haired bats moving north in the spring and south in the fall (Johnson et al. 2011), although this could reflect foraging activity variations due to insect population fluxes. In Hawaii, hoary bats apparently perform a seasonal altitudinal migration, with both sexes moving to lowlands during breeding season and then returning to highlands for the remainder of the year (Menard 2001). Seasonal altitudinal migration is also suggested for hoary bats in the Galapagos Islands (McCracken et al. 1997).

15.4.2 Regional Migrant Cave Bats: Schreiber's Bats

Many cave-roosting bats tend to move shorter distances, 500 km or less, and with less of a standard compass orientation than tree bats and in the spring, many species radiate from common hibernacula in a star-shaped pattern (Hutterer et al. 2005).

The cave-roosting regional migrant Schreiber's bent-winged bat (*Miniopterus schreibersii*) is one of the most widespread species, in Europe, Africa, and Australia. Genetic structure occurs between subpopulations in southeastern Europe (Bilgin et al. 2008) and Australia (Cardinal and Christidis 1999) and existence of the closely related *Miniopterus natalensis* in South Africa (Miller-Butterworth et al. 2005).

The combination of strong philopatry and extensive banding has resulted in details of seasonal movements. In Portugal (1987–2005), 36,000 bats were banded and tracked (Ramos Pereira et al. 2009; Rodrigues and Palmeirim 2008, Rodrigues et al. 2010) providing evidence that females stage at spring roosts until just before parturition when they move to maternity roosts in caves. Following weaning, they move to other caves where they spend autumn and sometimes winter. Males leave hibernacula later and change roosts during maternity season, and roost temperature was more likely to influence migration destination than insect availability, as inferred from temperatures at foraging areas (Rodrigues and Palmeirim 2008).

While many migratory bat species show little evidence of population structure (Petit and Mayer 2000; Russell et al. 2005), Schreiber's bat is an interesting exception and extensive banding data enable us to compare population structural and observed behavior to predictive models (Ruedi and McCracken 2009). For example, strong patterns of structure in mitochondrial DNA (mtDNA) are considered to indicate strong female philopatry to breeding sites, and more diffuse patterns in males indicate sex-biased movement by males during breeding seasons. In this scenario, nuclear DNA (nDNA) patterns would not show structure. In the Portuguese Schreiber's bat colonies, while both males and females visit different maternity caves, all females raise pups only in the cave in which they were born (Rodrigues et al. 2010). Mating occurs at hibernacula shared among the colony's maternity roosts (Rodrigues and Palmeirim 2008). As a result of this strict philopatry to maternity caves, all gene flow is male-induced during regional migrations (Rodrigues

et al. 2010). The strong patterns in mtDNA also appear, at a weaker level, in nDNA, reflecting the strong regional philopatry observed in both males and females (Ramos Pereira et al. 2009).

In a study of the closely related South African Schreiber's long-fingered bat (*M. natalensis*), Miller-Butterworth et al. (2003) found similar population structure even though migration varied between subpopulations. However, neither migration distance nor zoogeographic barriers prevented gene flow between colonies, so structure was due to philopatry or other differences. In one subpopulation, morphological differences mirrored the genetic distinctions, with the northern colony (intermediate migrants) showing higher wing aspect ratios than other colonies (shorter-distance migrants) (Miller-Butterworth et al. 2003).

15.4.3 Long-Distance, Facultative, and Partial Migrants

Migratory patterns of Brazilian free-tailed bats (*Tadarida brasiliensis*) are more difficult to define than for the tree and cave bats described above. In contrast to the highly structured populations of *M. schreibersii*, populations of Brazilian free-tailed bats are panmictic, showing no genetic structure (Russell et al. 2005), but bats in different geographic areas demonstrate different migratory behaviors. In the southeastern USA, they appear to be sedentary and to use torpor in winter (Cockrum 1969; Laval 1973), whereas on the west coast, bats probably migrate but not necessarily long distances or in a north–south direction (Kruttsch 1955). In mid-continent a large segment of the population are long-distance migrants, traveling up to 1,900 km between Mexico and the USA (Cockrum 1969; Glass 1982); however, many males may remain in Mexico year-round (Davis et al. 1962; Glass 1982), while other males move north where they mate in the spring in Texas (Reichard et al. 2009). Reports of large maternity colonies in Mexico (Lopez-Gonzalez and Best 2006) and of bats overwintering in the USA (Geluso 2008; Scales and Wilkins 2007) further confuse the picture.

Bats overwintering at Carlsbad Cave, New Mexico, included individuals of both sexes and varying ages, and evidence indicates active feeding in winter except during high winds (Geluso 2008). Banding of large numbers in the 1950s and 1960s (Cockrum 1969; Glass 1982; Villa and Cockrum 1962) showed migration between caves in the southwestern United States and Mexico. Bats leaving nursery caves in Oklahoma range into Texas and Mexico during the fall, traveling as far as 1,840 km, and do not return until the spring (Glass 1982). The maximum documented migration rate was 32 km/day (Villa and Cockrum 1962). Cold weather appears an important factor spurring fall bat movement (Constantine 1967; Svoboda and Choate 1987). Brazilian free-tailed bats change roosts frequently before and after the maternity season with population sizes fluctuating greatly in caves in Kansas during spring (Twente 1956), and Davis Cave in South Central Texas is a staging area in spring for bats going north to Oklahoma caves (Short et al. 1960). In the fall, populations shift from caves to nearby bridges (Horn and Kunz 2008).

The considerable variation in migration strategies found in Brazilian free-tailed bats may be analogous to Blackcaps (*Sylvia atricapilla*) found across Europe and Africa which show wide variations in migratory strategies with very little population structure (Perez-Tris et al. 2004).

15.4.4 Migration in Old-World Fruit Bats

Even less is known about migration of old-world fruit bats than for microchiropterans, and there are undoubtedly many migratory pteropodids as yet unstudied (Fleming and Eby 2003). Most documented migration by fruit bats is regionally restricted, nondirectional, and tracks ephemeral food resources (Fleming and Eby 2003), except for the straw-colored fruit bat (*Eidolon helvum*). At least one population of these large bats leaves their African savanna habitat during the dry season and moves 2,518 km (Richter and Cumming 2008) to take advantage of large fruiting events (Richter and Cumming 2006). Between five and ten million *E. helvum* spend October through December at Kasanka National Park, Zambia, arriving as fruit ripens and leaving when fruiting slows (Richter and Cumming 2006). It is unclear whether this foraging pressure is sustainable, as areas are becoming degraded, resulting in higher tree mortality and fire risk (Byng et al. 2010). Richter and Cumming (2008) tracked four male *E. helvum* with satellite transmitters from Kasanka back to the Democratic Republic of Congo and showed that bats moved an average of 90 km/day and traveled 2,518 km in 149 days. Thomas (1983) suggests this movement is to avoid competition for fruit resources.

Other examples of wide-ranging movements of pteropodids are less obviously migratory. A number of *Pteropus* species have been studied as reservoirs for viral pathogens; at least three *Pteropus* species are known to harbor Hendra or Nipah viruses. Radiotracked *P. vampyrus* traveled across political borders in Southeast Asia (Epstein et al. 2009), including Thailand, Sumatra, Malaysia, and Indonesia, flying up to 363.4 km. One bat covered 130 km in 2 h while foraging (Epstein et al. 2009), and in another case, a *P. alecto* traveled over 3,000 km (Breed et al. 2010).

15.5 Future Directions

Our knowledge of migration in bats has been limited (Griffin 1970), but as new technologies are applied, knowledge will increase (Bridge et al. 2011; Cryan and Diehl 2009; Holland and Wikelski 2009).

Satellite tracking offers long-distance monitoring of individuals (Wikelski et al. 2007), but current transmitters are too large for most bats (Aldridge and Brigham 1988). However, exciting results are coming in from tracking large bats (Richter and Cumming 2008; Tidemann and Nelson 2004). Smith et al. (2011) found that optimal tracking design for *Pteropus* was species- and ecology-specific with solar

powered transmitters only working for bats that roost higher in canopy, allowing for recharging during the day.

Stable isotopes can infer movements of individual bats over long distances because stable hydrogen isotopes (δD) are absorbed into tissues and fur from water. By matching isotope values from tissue samples with known values from water sources across a landscape, one can determine at what location those tissues formed. Stable hydrogen isotope (δD) values from the hair of bats (captures or museum collections) identified movement patterns of North American tree bats (Britzke et al. 2009; Cryan et al. 2004). Fraser et al. (2012) showed that contrary to previous assumptions, male *Perimyotis subflavus* migrated in north–south directions like hoary or silver-haired bats, rather than as regional migrants. Despite the usefulness of stable isotopes, there are important limitations; quantifying underlying hydrogen isotope gradients in water supplies is needed to provide more meaningful spatial resolution. In addition, understanding molt patterns is critical because species vary in annual molt cycles thereby affecting δD values (Fraser et al. 2010), although using δD values from hair from sedentary bat species avoids the molt-timing problem (Popa-Lisseanu et al. 2012). In that study, when combined with $\delta^{13}C$ and $\delta^{15}N$ values, δD values predicted locations of known bat samples significantly more accurately.

Advances in radar technologies allow tracking the movements of individuals and groups of individuals and possibly to distinguish among taxa (Ahlen et al. 2009; Chilson et al. 2011; Gauthreaux et al. 2008; Horn and Kunz 2008, but see Kunz et al. 2007). Bruderer and Popa-Lisseanu (2005) compared video and radar data to differentiate small, medium, and large bats from migrating birds, although distinguishing among similar-sized bats (e.g., *Nyctalus noctula* and *Eptesicus serotinus*) required analysis of additional behavioral or ecological features. Their data also showed that during migration, flight speeds for *N. noctula* and *E. serotinus* were higher than expected. Study-specific radar installations are not necessarily required to apply this technology to broader questions of bat migration. The newly developed National Mosaic and Multi-Sensor Quantitative Precipitation Estimation system (NMQ) Web portal offers public access to NEXRAD historical data that will enable tracking of migrants across North America (Chilson et al. 2011), but much work needs to be done to standardize the data sets for biological use.

We believe the following will be at the forefront of future migration research on bats: (1) placing bats in the theoretical context of migration; (2) understanding the physiology of energy storage and use during migration; (3) exploring links between seasonal and spatial changes in food availability, the timing of migration events, and the use of stopover locations in bats; (4) documenting long-distance movements of individual bats across international boundaries and establishing connectivity of their populations through use of satellite technology; and (5) learning more about individual and group movements and assessing population sizes and trajectories using information from radar networks. The continued growth of wind power and its impact on bat populations as well as effects of climate change on the movements of bats, their prey, and the pathogens that they vector all suggest that migration in bats will be an increasingly important focus of research.

Acknowledgments The authors thank Paul Cryan, Erin Baerwald, and Liam McGuire for discussions and invaluable feedback that greatly improved the quality of this chapter.

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