

Altitudinal migration in bats: evidence, patterns, and drivers

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ABSTRACT

Altitudinal migrations are common in all major vertebrate and some invertebrate lineages. Such migrations have important implications for the basic and applied ecology of animals making these movements. The idea that bats make altitudinal migrations has been suggested for nearly a century. However, studies documenting the existence and causes of altitudinal bat migrations are scarce, and are frequently published in the ‘grey’ literature. For the first time, we comprehensively review the evidence supporting the existence of altitudinal bat migrations worldwide, describe basic patterns of migration in temperate and tropical regions, and articulate and propose tests of hypotheses potentially explaining these migrations. We compiled a list of 50 studies indicative of altitudinal bat migration in 61 species (five families) from 21 countries (four continents). The temporal and spatial patterns of these migrations grouped biogeographically. Temperate bats generally exhibit sex-biased migrations with females inhabiting lower elevations than males during reproductive periods. Although there is less information on tropical bat migration, few studies report sex-biased migration. We compiled hypotheses proposed in the bat and (more extensive) avian literature to provide a list of hypotheses potentially explaining altitudinal bat migrations. These hypotheses rely upon temporal availability of (and competition for) food resources, spatial distribution of geomorphological features suitable for hibernation, sex-related differences in the use of torpor, mating opportunities, and climatic factors that impose direct physiological challenges to survival or that restrict the ability to forage. A more thorough description of the migration patterns of most species will be required to distinguish effectively among these hypotheses. We identify research avenues that would broaden our understanding of bat migration patterns and provide critical information required for effective conservation.

Key words: partial migration, differential migration, sexual segregation, bats, chiroptera, evolution of migration, seasonal movements.

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I. INTRODUCTION

Interest in all aspects of bat migration has increased in recent years (Popa-Lisseanu & Voigt, 2009). Migration has evolved independently in multiple lineages, and short- and long-distance migration likely evolved independently rather than sequentially (Bisson, Safi & Holland, 2009). Current reviews of bat migration have used arbitrarily defined short- and long-distance movement thresholds that do not allow for the integration of even shorter distance movements (i.e. < 100 km) into the theoretical and practical frameworks developed for longer-distance movements (Fleming & Eby, 2003). However, consideration of these shorter-distance migrations, especially altitudinal migration, may lead to new insights into the evolution and maintenance of migratory systems. Altitudinal migration commonly refers to annual return movements of all or part of an animal population between breeding and non-breeding areas that differ in elevation (Dixon & Gilbert, 1964; Rabenold & Rabenold, 1985). Altitudinal migrations often occur over short spatial scales involving few physiological adaptations, and consequently, are frequently overlooked in studies of the causes and consequences of seasonal migrations. However, from the standpoint of understanding the underlying ecological and evolutionary factors influencing migratory decisions, these cyclical, seasonal movements parallel longer-distance latitudinal migrations in most important respects. They also pose similar challenges to devising effective species-level conservation strategies (Powell & Bjork, 1995). Unfortunately, there is scant basic knowledge regarding the number of species that migrate altitudinally, the temporal and geographical patterns of such migrations, and the reasons for inter- and intra-specific variation in migratory tendency in most taxonomic groups. Altitudinal migrations have been reported from all continents except Antarctica, and in many terrestrial animal lineages including ungulates (Hebblewhite & Merrill, 2009; Mysterud, 1999; Rice, 2008), carnivores (Loucks *et al.*, 2003), lepidopterans (Stefanescu, 2001; Haber & Stevenson, 2004), hymenopterans (Hunt *et al.*, 1999), and many orders of birds (e.g. Ramos-Olmos, 1983; Loiselle & Blake, 1991; Sick, 1993; Johnson & Maclean, 1994). However, only in birds have altitudinal migration patterns and the factors driving these patterns been studied in detail, and even then in only a handful of species. Despite the fact that among bat researchers only relatively long-distance movements are commonly referred to as ‘migration’, numerous sources mention seasonal altitudinal movements of bats around the world (e.g. Hutson, Mickleburgh & Racey, 2001). Yet close scrutiny of citations purportedly providing evidence for altitudinal bat migrations reveals that these papers often contain very weak evidence, and/or consist of

conjecture and speculation. For instance, Sanborn & Crespo (1957) is an oft-cited reference used to support the existence of altitudinal migration in South American hoary bats *Lasiurus cinereus villosissimus*. Yet the statement made by the authors (translated from Spanish) is simply: ‘It is possible that ... the Chilean individuals engage in altitudinal migrations, ... and the Colombian and Venezuelan ones either altitudinal migration or no migration’. (Sanborn & Crespo, 1957, p. 10). Evidence backing this statement comes from nine specimens collected during the breeding season at lower elevations in Chile, a lack of records further north along the westward side of the Andes, and ten specimens collected from Colombia and Venezuela at various elevations [see Findley & Jones (1964) for these data plotted on a map]. Note also that Sanborn & Crespo (1957) presented the idea of altitudinal migration tentatively, using the word ‘possible’. Thus, while it is plausible that hoary bats and other species do indeed engage in altitudinal migrations, a critical evaluation of the evidence is overdue.

Bats are ideally suited for comparative studies of migration evolutionary ecology. Like birds, they are small, endothermic, flying vertebrates. Thus, their behaviours have been independently shaped by many of the same morphological and physiological constraints as their better-studied avian counterparts. However, being mammals, they differ in some key respects that likely influence the trade-offs involved in migratory decisions: (i) bat embryos develop inside their mothers adding to the costs of flight during pregnancy; (ii) female bats incur substantial energetic costs of producing milk for nursing young; (iii) in some species, females store sperm (Crichton, 2000) which permits temporal and spatial asynchrony between mating (when sexes must be sympatric) and raising young (when sexes can be allopatric) and (iv) many species are capable of using torpor, greatly reducing energetic costs during inclement weather. These traits can explain both similarities and differences in results from the bird and bat literature investigating the physiological ecology and energetics of long-distance migrant species breeding in North America (McGuire & Guglielmo, 2009; McGuire *et al.*, 2012). The extent to which patterns of bat migration parallel or diverge from those of altitudinal migrant birds would considerably advance our understanding of the ecological and physiological factors that are important generally in shaping and driving altitudinal migration.

The objectives of this study are threefold: (i) compile and critically evaluate the evidence for bat altitudinal migrations *via* a thorough literature search; (ii) synthesize the hypotheses that could explain patterns in this body of literature, drawing from knowledge of the avian literature and (iii) formulate a series of testable predictions to distinguish among the possible

explanations potentially shaping these migrations. We hope that this review both clarifies the state of our knowledge of altitudinal bat migration and inspires more researchers to study this poorly understood topic. We begin with a brief review of the patterns and proposed drivers of altitudinal bird migration, using this as a basis for interpreting bat migrations.

II. A BRIEF REVIEW OF BIRD ALTITUDINAL MIGRATION

The study of migration in any taxonomic group and geographical area begins with documenting local seasonal fluctuations in abundance, and then identifying the spatial and temporal patterns of movements. These basic patterns must be elucidated before it is possible to answer questions regarding the ecological, physiological, and evolutionary causes and consequences of migration. In the avian literature, the first stages of this process began three-quarters of a century ago, and were primarily driven by monographs on bird distribution and abundance in a few tropical localities (e.g. Beebe, 1947; Slud, 1964; Skutch, 1967). Earlier references to altitudinal migrations in temperate-zone mountains (e.g. Presnall, 1935; Grinnell & Miller, 1944) failed to attract the interest that their tropical counterparts did, perhaps because the seasonal disappearance of birds from frigid temperate mountains was less surprising to temperate-zone biologists than was the seasonal movement of birds up and down tropical mountains. The majority of the literature on avian altitudinal migration still consists of documenting patterns consistent with the occurrence of altitudinal migration obtained *via* direct observations (e.g. Ferrari *et al.*, 2008), mark-recapture data derived from mist-netting and banding (e.g. Burgess & Mlingwa, 2000), or more recently, stable isotope data (e.g. Hobson *et al.*, 2003; Fraser, Kyser & Ratchliffe, 2008) and radio-tracking (Powell & Bjork, 2004). These data come primarily from the northern Neotropics [especially Costa Rica (Stiles, 1988) and Mexico (Ornelas & Arizmendi, 1995)], Brazil (Bencke & Kindel, 1999; Alves, 2007), South Africa (Johnson & Maclean, 1994; Symes, Wirminghaust & Downs, 2002), and to a lesser extent temperate North America (Rabenold & Rabenold, 1985; Morrissey, Bendell-Young & Elliott, 2004), Europe (Saniga, 1995), Australasia (Green, 2006), and other parts of South America (Hilty, 1997). Evidence for altitudinal bird migration now exists for most major mountain ranges of the world.

Relatively few avian systems have been sufficiently well characterized to permit studies aimed at understanding why and how these migrations occur, and why they occur in some but not all taxa living in a particular region. The proposed causes of altitudinal migration involve spatial and temporal variation in food availability (Rabenold & Rabenold, 1985; Levey & Stiles, 1992), predation risk (Boyle, 2008a), nest-site limitation (Mackas *et al.*, 2010), or climatic conditions (Skutch, 1969; Boyle, Norris & Guglielmo, 2010). More than

one factor may contribute to shaping migration patterns. For instance, different factors likely govern uphill and downhill portions of the migration cycle in many species because the factors making one elevation suitable for reproduction may not make it the best elevation for survival during the non-breeding season.

The costs and benefits of alternative migratory strategies have been studied in detail in only a handful of bird species including American dippers *Cinclus cinclus* in Pacific coastal mountains of Canada (Morrissey, 2004; Middleton, Morrissey & Green, 2006; Gillis *et al.*, 2008; Middleton & Green, 2008; Mackas *et al.*, 2010), and white-ruffed manakins *Corapipo altera* in wet tropical forested mountains in Costa Rica (Rosselli, 1994; Boyle, 2008b, 2010; Boyle *et al.*, 2010, 2011). Because these species serve as a reference for comparisons with tropical and temperate bat species, we briefly describe the major aspects of these migrations.

American dippers range from Alaska to Central America in western mountains, feeding on fish fry and aquatic invertebrates (Willson & Kingery, 2011). Populations in southern British Columbia consist of resident individuals that breed and over-winter on low-elevation rivers, and migrant individuals that breed along high-elevation streams, descending to low-elevation rivers to over-winter with residents (Morrissey *et al.*, 2004). Migrants have access to inferior food resources during the breeding season which results in poorer nestling condition (Mackas *et al.*, 2010). Migrants also experience similar rates of nest predation relative to residents (Morrissey, 2004). Residents initiate nesting earlier each year, are more likely to rear a second brood, and consequently raise more young (Morrissey, 2004). Despite slightly lower annual survival, residents achieve greater lifetime reproductive success (Gillis *et al.*, 2008). The most plausible hypothesis explaining altitudinal migration in this species is that competition for food and/or limited breeding territories forces some individuals to breed at higher-elevation (inferior) sites that are unsuitable for year-round residency due to climatic factors that not only pose direct physiological challenges to survival but make access to food impossible.

Migration patterns of frugivorous white-ruffed manakins living in the mountains of Central America contrast with American dippers in many regards. Costa Rican Caribbean-slope populations of this species consist of residents that remain at montane breeding sites year-round and migrants that breed together with residents, but then migrate downhill, spending a few to several months of the non-breeding season at low elevations (Rosselli, 1994). Breeding location and timing coincides with maximum food availability, but food availability cannot explain downhill migration (Boyle, 2010). Migration is male-biased and related to condition (Boyle, 2008b). Higher-elevation breeding sites receive twice as much rain and more severe rain storms than the adjacent lowlands. Males that remain at high elevations year-round suffer more severe adverse effects of storms (Boyle *et al.*, 2010), but accrue reproductive advantages *via* increased social status and the ability to attract females

the following year (Boyle *et al.*, 2011). The most plausible hypothesis explaining altitudinal migration in this species is that montane rainstorms force energetically challenged individuals downhill *via* limited foraging opportunities during storms with consequent survival benefits and reproductive costs.

The two species' migrations described above exemplify some general patterns evident in the broader avian literature. First, climatic differences between high and low elevations play a role in shaping migration patterns. Second, among tropical altitudinal migrants, most species are frugivorous or nectarivorous, an observation that initially led to several tests of food-based hypotheses explaining tropical altitudinal migration (Rosselli, 1994; Solórzano *et al.*, 2000; Chaves-Campos, 2004). Third, interactions between environmental conditions and individual physiology shape migratory decisions: in neither American dipper nor white-ruffed manakin does food availability, predation risk, or climate affect migration tendency in simple, straightforward ways. Finally, partial migration (only a portion of the population migrates) or differential migration (demographic groups migrate different distances) is common among avian altitudinal migrants and is often sex-biased (Stiles, 1988; Johnson & Maclean, 1994). This last point implies that facultative migration decisions can mediate life-history trade-offs in a dynamic fashion. Such flexible migration systems are thus particularly valuable for identifying ecological factors leading to the evolution of migratory behaviour in general. After presenting what is known of bat altitudinal migration patterns, we will return to these generalities and examine the extent to which the processes apparently shaping avian altitudinal migration may also shape bat altitudinal migration.

III. EVIDENCE: DO BATS MIGRATE ALTITUDINALLY?

Despite frequent mention of altitudinal migration in the bat literature, few studies have focused on these movements explicitly. Several studies have examined changes in bat communities with elevation (e.g. McCain, 2007) but treat altitudinal distribution as a fixed trait of species or populations, ignoring possible seasonal movements. Much of the literature pertaining to altitudinal bat migration is anecdotal or speculative, and is found in regional journals or grey literature sources. Furthermore, altitudinal migration is rarely referred to as such in the bat literature. More frequently, authors refer to seasonal distributional shifts, seasonal invasions, elevational movements, altitudinal shifts, or sexual segregation. Thus, we began by conducting a thorough literature search using standard online search engines (i.e. *Web of Science*, *Google Scholar*) for evidence of altitudinal migration by bats worldwide. We started with reviews of bat migration (e.g. Griffin, 1970; Fleming & Eby, 2003; Hutterer *et al.*, 2005) and followed chains of references from those sources to expand our database. This effort

produced 50 papers that contained evidence, discussion, or speculation regarding altitudinal migrations in 61 species of bats belonging to five families (Table 1). These reports came from around the world (i.e. North America, Central and South America, Eastern and Western Europe, Asia, Pacific Islands) and were published in English, Spanish, Portuguese, French, German, and Chinese. We may have missed relevant literature from Asia, Africa, Eastern Europe, and elsewhere if such sources were not referenced by other authors, were not discoverable *via* our search methods, or due to linguistic limitations of the authors.

(1) Patterns: who, when, and where?

Two broadly different patterns of altitudinal migration emerge from this literature. The first pattern was common in temperate species, while the second was generally (but not exclusively) associated with tropical or sub-tropical species. Accordingly, we deal with these groups separately below. Where temperate/tropical categorization was ambiguous, we discuss those species based on ecological and phylogenetic affinities. For example, the lesser long-nosed bat *Leptonycteris yerbabuenae*, a nectarivore (Family Phyllostomidae), ranges from Mexico north to southern Arizona. The populations reaching Arizona migrate altitudinally in patterns resembling those of tropical species, and hence, we discuss this species together with species making similar migrations.

(a) Temperate patterns

The idea that temperate bats migrate altitudinally dates back a century. The very first article published in the *Journal of Mammalogy* (volume 1, issue 1, page 1; Allen, 1919) describes the possibility of a 'local and seasonal invasion by the non-breeding individuals' of 'the upper levels of mountains'. A year earlier, upon finding only female and young Yuma myotis *Myotis yumanensis* at lower elevations, Grinnell (1918) suggested that in summer, non-breeding males may move to higher elevations to forage. However, neither of these authors provided direct evidence of altitudinal bat migration. Today, several studies provide convincing evidence of altitudinal migration in temperate regions. One of the best examples comes from big brown bats *Eptesicus fuscus* in Colorado. Radiotracking bats between summer and winter roosts, Neubaum *et al.* (2006) confirmed that bats (primarily females) migrate to lower elevations for the summer and return uphill to the mountains to hibernate in winter. Similarly, band recoveries of Townsend's big-eared bats *Corynorhinus townsendii* in the Black Hills of South Dakota indicate that females migrate from high-elevation hibernacula to low-elevation summer roosts (Cryan *et al.*, 2000). Sex-biased differential altitudinal migration has also been suggested for little brown bats *Myotis lucifugus* in the Rocky Mountains, Alberta, Canada (Barclay, 1991). Likewise, Daubenton's bat *Myotis daubentonii* in Switzerland migrate downhill in the spring and return uphill in autumn, presumably to high-elevation hibernacula (Leuzinger & Brossard, 1994). All females in this Swiss population appear to migrate,

Table 1. Summary of literature reporting or discussing altitudinal bat migration, listed by family and species

Taxon	Location	References	Nature of data
Vespertilionidae			
<i>Corynorhinus townsendii</i>	South Dakota, USA California & Nevada, USA	Cryan, Bogan & Altenbach (2000) Szewczak <i>et al.</i> (1998)	Band recoveries Hibernating range at higher elevation than summer range
<i>Eptesicus fuscus</i>	California, USA Colorado, USA	Allen (1919) Neubaum, O'Shea & Wilson (2006) O'Shea <i>et al.</i> (2011b)	Only male captures at high elevation Radio-tracking, passive integrated transponder detections, altitudinal based sex bias Female bias at low elevation in summer, male bias at high elevation in summer
	South Dakota, USA Texas, USA Washington, USA	Cryan <i>et al.</i> (2000) Easterla (1973) Thomas (1988) Baker & Lacki (2004)	Variation in sex bias along altitudinal transect Altitudinal sex segregation Only males at higher elevation in one mountain range but not others
	British Columbia, Canada	Fenton <i>et al.</i> (1980) Grindal, Morissette & Brigham (1999)	Male bias at high elevation Male bias at higher elevation Altitudinal sex segregation of several species combined, species-specific patterns not presented
<i>Eptesicus nilssonii</i>	Germany	Holzhaider & Zahn (2001)	Male bias at higher elevations, maternity colonies only at lower elevation
<i>Eptesicus serotinus</i>	Slovakia	Kaňuch & Krištín (2006)	Altitudinal sex segregation
<i>Lasionycteris noctivagans</i>	South Dakota, USA Arizona, USA	Cryan <i>et al.</i> (2000) Cockrum & Ordway (1959) Hoffmeister (1970)	Variation in sex bias along altitudinal transect Seasonal presence at different elevations Altitudinal migration suggested but no evidence
	Colorado, USA British Columbia, Canada	O'Shea <i>et al.</i> (2011b) Grindal <i>et al.</i> (1999)	Male bias at high elevation in summer Altitudinal sex segregation for all species combined but did not present species-specific patterns
<i>Lasiurus blossevilli</i>	California, USA	Grinnell (1918)	As <i>Nycteris borealis</i> ; seasonal capture records: in summer females at low elevation, males at higher elevations. Explicitly suggests altitudinal migration
	Galapagos Islands, Ecuador	McCracken <i>et al.</i> (1997)	<i>Lasiurus blossevilli brachyotis</i> ; altitudinal sex segregation in non-breeding season, limited seasonal acoustic monitoring
<i>Lasiurus cinereus</i>	South Dakota, USA Galapagos Islands, Ecuador	Cryan <i>et al.</i> (2000) McCracken <i>et al.</i> (1997)	Variation in sex bias along altitudinal transect Limited seasonal acoustic monitoring; cited by Hutson <i>et al.</i> (2001) and Menard (2001)
	Hawai'i, USA	Bonaccorso <i>et al.</i> (2009), Todd <i>et al.</i> (2009), Pinzari, Bonaccorso & Gorresen (2009) and Menard (2001)	Regular seasonal acoustic monitoring across altitudinal gradient Seasonal observations at multiple elevations, seasonal sex-bias change in lowlands
	California, USA	Dalquest (1943) and Vaughan & Krutzsch (1954)	Capture and museum records indicate seasonal absence, altitudinal sex segregation
	Colorado, USA Chile, Colombia, Venezuela	O'Shea <i>et al.</i> (2011b) Sanborn & Crespo (1957)	Male bias at high elevation in summer Seasonal capture records; Findley & Jones (1964), McCracken <i>et al.</i> (1997), Hutson <i>et al.</i> (2001) and Menard (2001) cite speculation in Sanborn & Crespo (1957)

Table 1. Continued

Taxon	Location	References	Nature of data
<i>Murina bicolor</i>	Taiwan	Cheng <i>et al.</i> (2009)	High-elevation hibernation, only found at low elevations in summer
<i>Myotis brandti</i>	Germany	Holzhaider & Zahn (2001)	Male bias at higher elevations
<i>Myotis californicus</i>	British Columbia, Canada	Fenton <i>et al.</i> (1980) Grindal <i>et al.</i> (1999)	Male bias at higher elevation Altitudinal sex segregation for several species combined, species-specific patterns not presented
	Washington, USA	Thomas (1988)	Only males at higher elevation in one mountain range but not others
	Colorado, USA	Baker & Lacki (2004) O'Shea <i>et al.</i> (2011a)	Male bias at high elevation Reproductive females rare at high elevation
<i>Myotis ciliolabrum</i>	South Dakota, USA	Cryan <i>et al.</i> (2000)	Variation in sex bias along altitudinal transect
	Washington, USA	Thomas (1988)	Only males at higher elevation in one mountain range but not others
	Colorado, USA	Baker & Lacki (2004) O'Shea <i>et al.</i> (2011a)	Male bias at high elevation Reproductive females rare at high elevation
<i>Myotis daubentonii</i>	Switzerland	Leuzinger & Brossard (1994)	Seasonal altitudinal sexual segregation
	Italy	Russo (2002)	Seasonal altitudinal sexual segregation
	Germany	Encarnaç�o <i>et al.</i> (2005)	Seasonal altitudinal sexual segregation
	England	Senior, Butlin & Altringham (2005)	Seasonal inter- and intra-sex altitudinal segregation
	Slovakia	Kaňuch & Krist�n (2006)	Altitudinal sex segregation
<i>Myotis emarginatus</i>	Germany	Holzhaider & Zahn (2001)	Male bias at higher elevations
<i>Myotis evotis</i>	British Columbia, Canada	Grindal <i>et al.</i> (1999)	Altitudinal sex segregation for all species combined, species-specific patterns not presented
	Washington, USA	Thomas (1988)	Only males at higher elevation in one mountain range but not others
	Colorado, USA	Baker & Lacki (2004) O'Shea <i>et al.</i> (2011a, b)	Male sex bias at high elevation Reproductive females rare at high elevation
<i>Myotis formosus</i> ^a	Taiwan	Cheng (2009) and Cheng, Fang & Chou (2010)	High-elevation hibernation, summer activity at low elevations
<i>Myotis lucifugus</i>	California, USA	Allen (1919)	As <i>Myotis albicinctus</i> ; only male captures at high elevation
	Colorado, USA	O'Shea <i>et al.</i> (2011b)	Female bias at low elevation in summer, male bias at high elevation in summer
	South Dakota, USA	Cryan <i>et al.</i> (2000)	Variation in sex bias along altitudinal transect
	Washington, USA	Thomas (1988)	Only males at higher elevation in one mountain range but not others
	Alberta, Canada	Baker & Lacki (2004) Barclay (1991)	Male sex bias at high elevation Seasonal sex bias at high elevation
	British Columbia, Canada	Grindal <i>et al.</i> (1999)	Altitudinal sex segregation for all species combined, species-specific patterns not presented
<i>Myotis myotis</i>	Switzerland	Jaberg & Guisan (2001)	Seasonal altitudinal effect in species distribution model
	Germany	Holzhaider & Zahn (2001)	Male bias at higher elevations
<i>Myotis mystacinus</i>	Germany	Holzhaider & Zahn (2001)	Male bias at higher elevations, maternity colonies only at lower elevation
<i>Myotis occultus</i>	Colorado, USA	O'Shea <i>et al.</i> (2011a)	Reproductive females rare at high elevation; radio-tracked female suspected to be moving downslope from winter to summer roost

Table 1. Continued

Taxon	Location	References	Nature of data
<i>Myotis rufomiger</i> ^a	Taiwan	Cheng <i>et al.</i> (2010)	High-elevation hibernation, summer activity at low and high elevation
<i>Myotis septentrionalis</i>	South Dakota, USA	Cryan <i>et al.</i> (2000)	Variation in sex bias along altitudinal transect
<i>Myotis thysanodes</i>	South Dakota, USA	Cryan <i>et al.</i> (2000)	Variation in sex bias along altitudinal transect
	Washington, USA	Baker & Lacki (2004)	Male bias at high elevation
<i>Myotis volans</i>	California, USA	Allen (1919)	As <i>Myotis longicrus</i> ; only male captures at high elevation
	South Dakota, USA	Cryan <i>et al.</i> (2000)	Variation in sex bias along altitudinal transect
	Washington, USA	Thomas (1988)	Only males at higher elevation in one mountain range but not others
	British Columbia, Canada	Baker & Lacki (2004) Fenton <i>et al.</i> (1980) Grindal <i>et al.</i> (1999)	Male bias at high elevation Male bias at higher elevation Altitudinal sex segregation for several species combined, did not present species-specific patterns
<i>Myotis watasei</i> ^a	Taiwan	Cheng (2009)	Hibernate at high elevation, summer at low elevation
<i>Myotis yumanensis</i>	California, USA	Grinnell (1918) and Allen (1919)	Only females and young at low elevation
	Washington, USA	Thomas (1988)	Only males at high elevation
	British Columbia, Canada	Fenton <i>et al.</i> (1980) Grindal <i>et al.</i> (1999)	Male bias at high elevations Male bias at higher elevation Altitudinal sex segregation for several species combined, species-specific patterns not presented
<i>Nyctalus leisleri</i>	Slovakia	Kaňuch & Krištin (2006)	Altitudinal sex segregation
<i>Parastrellus hesperus</i>	Arizona, USA	Hoffmeister (1970)	As <i>Pipistrellus hesperus</i> ; altitudinal migration suggested but no evidence
	Colorado, USA	O'Shea <i>et al.</i> (2011a)	Reproductive females rare at high elevation
<i>Perimyotis subflavus</i>	Mexico, Honduras	Davis (1959)	As <i>Pipistrellus subflavus veraecrucis</i> ; museum specimens suggest summer in lowlands and hibernation in high elevation caves and mines
<i>Pipistrellus pipistrellus</i>	Slovakia	Kaňuch & Krištin (2006)	Altitudinal sex segregation
	Germany	Holzhaider & Zahn (2001)	Male bias at high elevations, maternity colonies only at lower elevation
<i>Pipistrellus nathusii</i>	Germany	Holzhaider & Zahn (2001)	Male bias at high elevations
<i>Plecotus auritus</i>	Germany	Holzhaider & Zahn (2001)	Male bias at higher elevations
<i>Vespertilio murinus</i>	Germany	Holzhaider & Zahn (2001)	Male bias at higher elevations
Molossidae			
<i>Tadarida brasiliensis</i>	Mexico	Constantine (1967)	Males move to higher elevations than females, lower elevation in winter
Rhinolophidae			
<i>Rhinolophus hipposideros</i>	Austria	Hutterer <i>et al.</i> (2005)	Winter roosts in mountains, summer roosts in lowlands
Phyllostomidae			
<i>Anoura geoffroyi</i>	Nicaragua	Fraser, McKinnon & Diamond (2010)	Suggests altitudinal migration, no evidence

Table 1. Continued

Taxon	Location	References	Nature of data
<i>Artibeus concolor</i>	Ecuador	Hutson (2004)	No data, just statement of altitudinal migration to track fruit
<i>Artibeus lituratus</i>	Costa Rica	Timm & Laval (2000)	Seasonal absence from high-elevation site
<i>Artibeus obscurus</i>	Ecuador	Hutson (2004)	No data, just statement of altitudinal migration to track fruit
<i>Artibeus toltecus</i>	Nicaragua Costa Rica	Fraser <i>et al.</i> (2010) Timm & Laval (2000)	Suggests altitudinal migration, no evidence Seasonal variation in abundance at high-elevation site
<i>Carollia brevicauda</i>	Nicaragua Costa Rica	Fraser <i>et al.</i> (2010) Timm & Laval (2000)	Suggests altitudinal migration, no evidence Seasonal variation in abundance at high-elevation site
<i>Chiroderma salvini</i>	Nicaragua	Fraser <i>et al.</i> (2010)	Suggests altitudinal migration, no evidence
<i>Choeronycteris mexicana</i>	Mexico	Valiente-Banuet <i>et al.</i> (1996, 1997)	Suggests altitudinal migration by bats pollinating flowers
<i>Glossophaga soricina</i>	Nicaragua	Fraser <i>et al.</i> (2010)	Suggests altitudinal migration, no evidence
<i>Hylonycteris underwoodi</i>	Costa Rica	Timm & Laval (2000)	Seasonal variation in abundance at high-elevation site
<i>Leptonycteris nivalis</i>	Mexico	Valiente-Banuet <i>et al.</i> (1997)	Mainly about pollination (possibly by altitudinal migrant bats)
<i>Leptonycteris yerbabuena</i> ^a	Mexico SW USA, Mexico	Herrera-Montalvo (1997) Valiente-Banuet <i>et al.</i> (1996, 1997) Cockrum (1991) Rojas-Martínez <i>et al.</i> (1999)	Only males at high-elevation site Suggests altitudinal migration by bats pollinating flowers Seasonal occurrence records across large region Seasonal captures at high and low elevation
<i>Loncophylla robusta</i>	Ecuador	Hutson (2004)	No data, just statement of altitudinal migration to track fruit
<i>Micronycteris megalotis</i>	Ecuador	Hutson (2004)	No data, just statement of altitudinal migration to track fruit
<i>Mimon crenulatum</i>	Ecuador	Hutson (2004)	No data, just statement of altitudinal migration to track fruit
<i>Phyllostomus hastatus</i>	Ecuador	Hutson (2004)	No data, just statement of altitudinal migration to track fruit
<i>Platyrrhinus brachycephalus</i>	Ecuador	Hutson (2004)	No data, just statement of altitudinal migration to track fruit
<i>Platyrrhinus helleri</i>	Ecuador	Hutson (2004)	No data, just statement of altitudinal migration to track fruit
<i>Pygoderma bilabiatum</i>	Brazil	Esbérard <i>et al.</i> (2011)	Seasonal captures, multiple elevations
<i>Sturnira erythromos</i>	Argentina	Giannini (1999)	Seasonal captures, multiple elevations
<i>Sturnira lilium</i>	Argentina	Giannini (1999)	Seasonal captures, multiple elevations

Table 1. Continued

Taxon	Location	References	Nature of data
	Ecuador	Hutson (2004)	No data, just statement of altitudinal migration to track fruit
<i>Sturnira ludovici</i>	Nicaragua	Fraser <i>et al.</i> (2010)	Suggests altitudinal migration, no evidence
	Costa Rica	Timm & Laval (2000)	Seasonal absence from high-elevation site
<i>Sturnira mordax</i>	Nicaragua	Fraser <i>et al.</i> (2010)	Suggests altitudinal migration, no evidence
<i>Uroderma bilobatum</i>	Costa Rica, Panama	McCarthy <i>et al.</i> (2005)	Speculation of altitudinal migration, no data
	Ecuador	Hutson (2004)	No data, just statement of altitudinal migration to track fruit
<i>Vampyressa melissa</i>	Ecuador	Hutson (2004)	No data, just statement of altitudinal migration to track fruit
<i>Vampyroides caraccioli</i>	Ecuador	Hutson (2004)	No data, just statement of altitudinal migration to track fruit
Pteropodidae			
<i>Pteropus giganteus</i>	Nepal	Hutson (2002)	Suggestion of altitudinal migration in Himalayas
Unspecified taxa/general report			
	Global	Hutson <i>et al.</i> (2001)	IUCN report advising further consideration of altitudinal migration
	California, USA	Pierson, Rainey & Corben (2001)	Suggests upslope migration (increased activity by acoustic monitoring at high-elevation site) to take advantage of late-season productivity

For each species, we note the reference(s), geographic location of the study, and include a brief description of the data. The nature of these studies is extremely variable. Some provide direct empirical evidence of altitudinal migration, others do not explicitly invoke altitudinal migration but contain observations consistent with altitudinal migration, and some do not present any data or evidence, but contain speculation regarding possible altitudinal migrations.

^aThere is some taxonomic uncertainty in the status of these species. *Myotis rufomiger* and *Myotis watasei* may both be subspecies of *Myotis formosus*, or *M. rufomiger* may be a subspecies of *M. watasei*.

^b*L. yerbabuenae* was formerly considered a subspecies of *Leptonycteris curasoae*; *L. sanborni* is a junior synonym (Wilson & Reeder, 2005).

whereas males are partially migratory with some individuals remaining at high elevations throughout the summer with similar patterns in *M. daubentonii* living in England (Senior *et al.*, 2005), Italy (Russo, 2002), Germany (Encarnação *et al.*, 2005), and Slovakia (Kaňuch & Křištín, 2006).

Many bat species around the world hibernate at higher elevations than where they rear their young: *Corynorhinus townsendii* in Utah, USA (Szewczak *et al.*, 1998), lesser horseshoe bats *Rhinolophus hipposideros* in Austria (Hutterer *et al.*, 2005), and three species of Taiwanese vespertilionid bats (Cheng, 2009; Cheng *et al.*, 2009; Cheng *et al.*, 2010). In each of these cases, it is not yet known whether only females or both sexes make altitudinal migrations.

In California, USA, male western red bats *Lasiurus blossevillei* (Grinnell, 1918) and hoary bats *Lasiurus cinereus* (Vaughan & Krutzsch, 1954) apparently migrate locally to higher elevations in summer from low-elevation over-wintering sites while females remain at low elevations year-round. Other individuals (of this and other species) migrate latitudinally, yet like the California populations, the sexes segregate altitudinally in summer. In South Dakota, male *L. cinereus*

and silver-haired bats *Lasionycteris noctivagans* (both latitudinal migrants) are more common at high elevations than females, suggesting that following latitudinal migrations, males settle at higher elevation than females (Cryan *et al.*, 2000). Without more detailed knowledge of the migratory movements of these populations it is unclear whether sexual segregation during the summer months is analogous to the altitudinal migrations in other populations.

Most of these temperate-breeding species exhibit sex-biased migration resulting in females occurring at lower elevations than males during the summer resulting in altitudinal sexual segregation. Altitudinal sexual segregation is common in temperate bat communities (e.g. Howell, 1920; Constantine, 1967; Easterla, 1973; Fenton *et al.*, 1980; Thomas, 1988; Grindal *et al.*, 1999; Holzhaider & Zahn, 2001; Baker & Lacki, 2004; O'Shea *et al.*, 2011a, b). In each of these examples, adult males (and sometimes non-breeding females) are found at higher elevations while reproductive females predominate at lower elevations. The majority of the species considered in these reports would normally be considered regional migrants (e.g. *Myotis lucifugus*,

Myotis myotis) although others are typically characterized as sedentary (e.g. *Eptesicus fuscus*) or long-distance latitudinal migrants (e.g. *Lasiurus cinereus*, *Nyctalus leisleri*; Fleming & Eby, 2003). Because sexes must occur sympatrically to mate, species or populations with altitudinal sexual segregation likely represent additional partial altitudinal migrants.

(b) *Tropical/sub-tropical patterns*

Compared to the abundant circumstantial and anecdotal evidence for altitudinal migration in temperate bats, there are few data documenting altitudinal movements in tropical or sub-tropical regions. Studies of community composition changes across altitudinal gradients are fairly common [e.g. McCain (2007) and references therein], but study designs typically have not included seasonal dimensions capable of detecting altitudinal migrations (but see Sánchez-Cordero, 2001). Other reports refer to the possibility of altitudinal migration, but provide no evidence. For example, Hutson (2002) mentions that *Pteropus giganteus* might migrate up and down the Himalayas, and Fraser *et al.* (2010) attempted to document altitudinal bat migration using stable isotopes in Nicaragua but problems of small sample sizes resulted in ambiguous conclusions.

A handful of studies provide evidence of altitudinal bat migration in tropical regions. In Costa Rica, long-term capture records at a montane site reveal that several species are either completely absent for part of the year or show substantial seasonal changes in abundance: the great fruit-eating bat *Artibeus lituratus*, Toltec fruit-eating bat *Artibeus toltecus*, silky short-tailed bat *Carollia brevicauda*, little yellow-shouldered bat *Sturnira lilium*, and Underwood's long-tongued bat *Hylonycteris underwoodi* (Timm & Laval, 2000). These authors suggested that seasonal changes in abundance may represent altitudinal migration, as is common among birds at the same site (Powell & Bjork, 1995; Chaves-Campos, 2004). Similarly, altitudinal migration has been proposed to explain variation in seasonal abundances of *S. lilium* and hairy yellow-shouldered bats *Sturnira erythromos* in the Argentinian Andes (Giannini, 1999). Notably, neither of these studies makes any mention of biased sex ratios in contrast to studies of temperate bat communities.

A study in Brazil (Esbérard *et al.*, 2011) conducted extensive year-round sampling at multiple elevations to test for evidence of altitudinal migration in Ipanema broad-nosed bats *Pygoderma bilabiatum*. In regions where temperature varied seasonally *P. bilabiatum* was absent, or less common, at higher elevations during cooler seasons. The authors concluded that bats migrated altitudinally in response to seasonal climate variation, a conclusion supported by constant abundance in regions where climate did not vary substantially. Sex ratio was female-biased at higher elevations suggesting that males remained at lower elevations.

Perhaps the best example of altitudinal bat migration in tropical or sub-tropical regions is that of the lesser long-nosed bat *Leptonycteris yerbabuenae* (Cockrum, 1991). In the northern parts of this species' range (i.e. NW Mexico and SW USA),

L. yerbabuenae migrate latitudinally. However, altitudinal migration also appears to play a prominent role in the movements of this species during the summer. Reproductive females migrate northward in the spring (late March–early May), foraging at lower elevations on seasonally abundant flowers from columnar cacti. When pups become volant in mid-summer (June–July), females and young move to higher elevations (Cockrum, 1991). These migrations are sex-biased; males (and non-reproductive adult females) remain in the southern portion of the range until mid summer (June–July) following which they join the reproductive females at the northern high-elevation sites (Cockrum, 1991) before all returning south in the autumn (September–October). In some southerly breeding populations of *L. yerbabuenae* (i.e. Puebla and Oaxaca, Mexico) individuals are hypothesized only to migrate altitudinally (Valiente-Banuet *et al.*, 1996, 1997; Herrera-Montalvo, 1997; Rojas-Martínez *et al.*, 1999).

South American hoary bats *Lasiurus cinereus villosissimus* also likely migrate altitudinally. Sanborn & Crespo (1957) analyzed the location and timing of collections of *L.c. villosissimus* and interpreted plausible movement patterns based on those records. Based on seasonal absence from the Chilean lowlands, the proximity of those records to the Andes, and the wide altitudinal distribution of records from Colombia and Venezuela, Sanborn & Crespo (1957) suggested that *L.c. villosissimus* make altitudinal migrations on the western slopes of the Andes in Chile and northern S. America. This study was among the first to explicitly suggest that bats make altitudinal migrations and is frequently cited as evidence for altitudinal bat migration despite the aforementioned tentative wording in the original publication (see Section I).

On the Galapagos Islands, altitudinal migration may explain the temporal and spatial distribution of *L.c. villosissimus* and Galapagos red bats *Lasiurus blossevillii brachyotis*. Capture data for *L.b. brachyotis* revealed a female sex bias in the lowlands and male sex bias at high elevations during the cool season (McCracken *et al.*, 1997). Acoustic sampling of both species provides evidence of a seasonal increase in activity in the lowlands during the cool season consistent with females migrating to higher altitudes during the hot (breeding) season when heavy rainstorms are more frequent (McCracken *et al.*, 1997). Similarly, on the island of Hawai'i, visual observations, capture records, and acoustic monitoring reveal that Hawaiian hoary bats *Lasiurus cinereus semotus* migrate to higher elevations, above the cloud inversion layer, during the non-breeding season when rainfall peaks (Menard, 2001; Bonaccorso *et al.*, 2008; Pinzari *et al.*, 2009). This pattern appears to be more pronounced on the windward (wetter) side of the island and may be protandrous. Menard (2001) noted an even sex ratio in the lowlands during the breeding period, followed by a female bias in the post-breeding period suggesting the males migrate upslope in advance of females. On the leeward (drier) side of the island, bats remain common at lowland sites year-round, although activity increases at dry, high-elevation sites early in the rainy season (Bonaccorso *et al.*, 2008).

IV. DRIVERS: WHY DO BATS MIGRATE ALTITUUDINALLY AND WHY DO ONLY SOME MIGRATE?

(1) Asking the right questions

As the previous section demonstrates, the patterns of altitudinal bat migration can be relatively complex. In most cases it is likely that several factors contribute to shaping these patterns. Understanding the underlying ecological and evolutionary causes of bat migration patterns requires that we answer two related but distinct questions. The first question is why do bats migrate at all (i.e. why do they not just stay in the same location year-round?). In reality, this is better posed as two questions: why do bats migrate uphill, and why do they migrate back down? Seemingly straightforward explanations for movements in one direction may not explain return movements in the opposite direction. The other related question, is why do only some individuals (typically one sex) in a population or species migrate, or migrate different distances than the others? To fully explain migratory patterns, hypotheses must address both questions. Ultimately, hypotheses explaining migration rely on variation in few ecological factors, including food availability, physiological (especially energetic) consequences of weather, predation risk, habitat limitation, and/or competition for mates.

Food availability and competition for food underlie most explanations for migration in many taxa from fish (Gross, Coleman & McDowall, 1988), to mammals such as giant pandas *Ailuropoda melanoleuca* (Loucks *et al.*, 2003), to birds (Cox, 1968; Fretwell, 1980). If food drives altitudinal migration, animals should move to elevations of highest relative food availability – a prediction that does not necessarily lead to animal abundances tracking food abundances at a given location over time. Under some circumstances, abundant food is not ‘available’ due to territoriality (Fretwell, 1972), increased threat of predation (Rosenzweig & Abramsky, 1997), or inclement weather (Boyle *et al.*, 2010). When different sex and age groups form dominance hierarchies, food limitation as influenced by competition can lead to differences in altitudinal migration strategies among demographic groups (Ketterson & Nolan, 1976).

Physiological and energetic costs of cold temperatures undoubtedly influence migration patterns both generally and in altitudinal migrations specifically, especially in temperate-breeding species. Endothermic flying vertebrates incur both high energetic costs of surviving when temperatures drop below their thermal neutral zone, as well as high costs of carrying extra body mass in the form of fuel reserves to buffer against inclement weather. Small body size exacerbates these energetic challenges due to increasing heat loss per unit mass as body size declines (Calder, 1974). When sexes differ in body size, the energetic (fasting) consequences of these differences can help explain differences in migratory strategies among sexes (Ketterson & Nolan, 1976). In some bats, hibernation and use of daily torpor greatly reduce

energetic costs during periods of inactivity. With decreasing ambient temperature, the potential energy savings of using torpor increase, but the cost to rewarm to normal body temperature also increases [see Speakman & Thomas (2003) for a discussion of the consequences of ambient temperature on torpor energetics]. Therefore, the net energetic benefits of migration to areas with lower temperatures will depend on numerous factors related to torpor energetics such as the frequency of arousal, endogenous energy stores, roost microclimate, and the potential for passive re-warming.

Another factor hypothesized to affect migratory decisions in birds is temporal and spatial variation in predation risk (Greenberg, 1980; Lank *et al.*, 2003; Boyle, 2008a). Predation risk is generally not perceived as a major factor influencing bat evolutionary ecology (Barclay & Harder, 2003), although it is possible that, like nestling birds, pups are more susceptible to predators than adults, and females locate their maternal roosts accordingly. Without specific knowledge of the identity, distribution, and relative abundance of such predators, however, it is impossible to evaluate predictions based on a predation-based hypothesis for bats.

Limited availability of critical and patchily distributed habitats may also shape altitudinal migration patterns. Habitat requirements may vary seasonally, being associated with only breeding or overwintering. One critical habitat is a suitable hibernaculum, required by non-migratory temperate breeding bats. A difference in the elevation of critical habitats required at different times of year could explain part of the altitudinal migratory cycle.

Mate competition can shape altitudinal migration patterns *via* differences among individuals in the reproductive payoffs of different migratory decisions (Morbey & Ydenberg, 2001; Boyle *et al.*, 2011). Because female bats of some species can store sperm for many months (Crichton, 2000), any trait that enables males to gain reproductive advantages (possibly by being the first male a female mates with or having a longer period over which to mate repeatedly) may affect the timing and location of migration. This implies that even if food or climatic factors drive females to migrate altitudinally, males may also make those movements (although not necessarily at the same time as females) solely for reproductive reasons.

Altitudinal migration patterns can be explained by one or more of these basic underlying ecological factors (Cristol, Baker & Corbone, 1999). Below we evaluate what is known of temperate and tropical bat altitudinal migration in light of these potential drivers.

(2) Why do temperate bats migrate altitudinally?

(a) Why do (female) bats migrate downhill?

In that first *Journal of Mammalogy* paper, Allen (1919) suggested that females were not found at high elevations during the summer because reproductive demands constrained them to ‘their proper “life zone”’. Numerous authors have echoed Allen’s (1919) speculation in various versions of a hypothesis that we refer to as the ‘reproductive constraints hypothesis’. This hypothesis combines food limitation and

physiological consequences of weather by proposing that the energetic demands of pregnant and lactating females (Kurta *et al.*, 1989) prevent them from inhabiting higher elevations where temperatures are cooler and insect prey are less abundant or more variable (Cryan *et al.*, 2000). Wetter, cooler weather is associated with reduced food supply and reduced reproductive success (fewer reproductive females, delayed parturition dates, females in poor body condition) in insectivorous bats (Grindal, Collard & Brigham, 1992; Lewis, 1993). The reproductive constraints hypothesis proposes that the energetic challenges of cool temperatures and reduced prey availability represent two distinct but correlated factors. Males may be able to inhabit higher elevations by using torpor to save energy when temperature is low and/or food is in short supply. However, lowering body temperature has detrimental effects on foetal development (Grinevitch, Holroyd & Barclay, 1995; Cryan & Wolf, 2003; Willis, Brigham & Geiser, 2006) restricting torpor use in pregnant females. Although females may use torpor at the expense of longer gestation (Racey, 1973; Racey & Swift, 1981), increases in gestation time may be constrained by consequent reductions in time available for young to develop and acquire energy reserves to survive winter hibernation at temperate latitudes where the active season is short. Furthermore, in some foliage-roosting species, precocial young are left exposed in the roost while the mother forages. The limited thermoregulatory capacity of newborn pups (Klug & Barclay, *in press*) means that warmer temperatures at low elevations may increase pup survival.

The reproductive constraints hypothesis predicts sexual segregation during the breeding season, with pregnant and lactating females found at lower elevations and males and non-reproductive females at higher elevations. The migration and sexual segregation patterns elucidated thus far of *Eptesicus fuscus* (Neubaum *et al.*, 2006), *Myotis lucifugus* (Barclay, 1991), *Myotis daubentonii* (Russo, 2002; Senior *et al.*, 2005), and many other temperate species (e.g. Cryan, 2003) are consistent with the reproductive constraints hypothesis. However, food availability can apparently mitigate the physiological challenges of cold. In the Canadian Rocky Mountains, reproductive females of *M. lucifugus* leave high elevations in summer, but female long-eared myotis *Myotis evotis* remain at high elevations year-round (Barclay, 1991). Due to differences in foraging behaviour, more prey is available for *M. evotis* than *M. lucifugus*. Higher relative food availability may provide the additional energy required to enable female *M. evotis* to maintain normothermic body temperatures and successfully reproduce at higher elevations despite cooler temperatures.

An hypothesis similar to the reproductive constraints hypothesis has been proposed to explain the absence of reproductive females of several species from high elevations of coastal (but not interior) mountain ranges of the NW United States (Thomas, 1988). High-elevation coastal sites receive more (and more frequent) summer rain than interior sites. Summer rain could limit the foraging opportunities for insectivorous bats, especially energetically

challenged reproductive females. Under this variation of the reproductive constraints hypothesis, it is not the direct physiological effects of temperature, but rather climatic factors affecting foraging opportunities that lead to downhill migrations in some populations. This hypothesis is virtually identical to the limited foraging opportunities hypothesis proposed to explain white-ruffed manakin migration (Boyle, 2008b).

It is clear that high elevations of temperate mountains often experience weather and/or food availability incompatible with rearing offspring, and this fact likely drives the downhill migration of reproductive females to lower elevations during summer. Theoretically, weather and food availability could act independently. In practice, however, it is difficult to imagine how this might occur for temperate insectivorous species. Because aerial insect prey abundance is closely tied to weather, climatic conditions that would preclude foraging (rain, wind, cold) would also affect the abundance of prey, thus confounding the two hypotheses. One approach to distinguish between these hypotheses would be to determine patterns of altitudinal sexual segregation in a species whose prey and foraging activities are unaffected by short-term weather fluctuations. The reproductive constraints hypothesis would predict female-biased migration irrespective of food availability whereas the food availability and limited foraging opportunities hypotheses would predict no downhill migration. This prediction, in combination with associations between migratory tendency and both food and short- and longer-term variation in climatic variables could elucidate the underlying causes of female-biased downhill migration.

(b) *Why do females not remain at low elevations year-round?*

At least two hypotheses could explain why females migrate back uphill following reproduction. First, because all bats that remain in temperate regions year-round hibernate, uphill movements may function to locate suitable hibernacula. This hypothesis relies on habitat limitation to explain the uphill portion of the migratory cycle. Subterranean sites such as caves and abandoned mines are not uniformly distributed with respect to elevation, and many studies report hibernacula to be abundant in mountainous areas (Schowalter, 1980; Barclay, 1991; Szewczak *et al.*, 1998; Cryan *et al.*, 2000; Piksa, 2008; Piksa, Bogdanowicz & Tereba, 2011). Furthermore, cave temperature is partially determined by mean annual surface temperature which varies with altitude (Barry, 2008). Consequently, bats may migrate to caves at elevations where optimal temperature conditions are found. Several authors have suggested that short altitudinal migrations are all that would be necessary for female bats to move between suitable summer and winter habitats (Barclay, 1991; Cryan *et al.*, 2000; Neubaum *et al.*, 2006).

An alternative hypothesis for the return of females uphill relies on the phenology of food resources along elevational gradients. With increasing elevation, peak plant and insect productivity shifts temporally. Advancing phenological peaks

are thought to explain ungulate migration in temperate mountains (Mysterud *et al.*, 2001; Sawyer & Kauffman, 2011). Although this hypothesis has received little attention in the bat literature (but see brief mention in Pierson *et al.*, 2001) prey phenology could potentially contribute to both tropical and temperate altitudinal bat migrations, and warrants further investigation.

The hibernacula availability and food phenology hypotheses for autumn uphill migration in females make several contrasting predictions. A critical prediction of the hibernacula availability hypothesis is that in areas where bats migrate altitudinally, suitable hibernacula are not found at lower elevations. The food phenology hypothesis predicts that females would spend at least a few weeks foraging at high elevations prior to entering hibernacula, and that food availability during the pre-hibernation period is higher at higher elevations than at lower elevations. Such patterns should result in measurable differences in behavioural and physiological metrics reflective of fueling rates in bats foraging at high and low elevations (e.g. duration of foraging bouts, rates of mass gain, and concentrations of plasma triglycerides). If food phenology does not affect migratory patterns and migration is driven by the availability of hibernacula, then we would predict females to proceed directly to hibernacula upon upslope migration.

(c) *Why do males often differ from females in migratory strategy?*

There are at least three plausible explanations why male bats frequently adopt different migratory strategies than their female counterparts. These explanations in turn rely upon climatic effects on energetic strategies, competition for mates, and intra-specific competition for food.

The fact that pregnant females incur high costs (*via* foetal development) of torpor use relative to males may explain why females, but not males, migrate to lower elevations while males remain at higher elevations (the ‘low-maintenance male’ hypothesis; Weller, Cryan & O’Shea, 2009). In addition to mitigating the effects of bad weather, torpor may benefit males by limiting energy expenditures during inactive periods, resulting in a greater net energy gain for a given foraging effort (Speakman & Rowland, 1999). This energetic benefit has been suggested to explain migration or sex-ratio patterns in several studies (Barclay, 1991; Grindal *et al.*, 1999; Russo, 2002). Non-reproductive females are presumably subject to similar energy demands as males and thus are also predicted to occur at higher elevations. Cryan *et al.* (2000) found a higher proportion of non-reproductive females at higher elevations, but other studies (e.g. Leuzinger & Brossard, 1994; Grindal *et al.*, 1999) have found both reproductive and non-reproductive females at lower elevations. In addition to energetic benefits, increased torpor use at higher elevations may reduce predation risk if predation risk is greater during foraging than roosting (Grinevitch *et al.*, 1995; a.k.a., the ‘cautious male’ hypothesis, Weller *et al.*, 2009).

In birds, one factor hypothesized to lead to differential migration is sexual size dimorphism (Belthoff & Gauthreaux,

1991). Individuals of the larger sex are better able to endure the harsher climate at higher altitudes (or latitudes) because of the lower surface area to volume ratio. In vespertilionid bats females tend to be larger than males (Williams & Findley, 1979) thus predicting differential male-biased altitudinal migration, opposite to observed patterns. Sexual size dimorphism in bats may predispose males to being more heterothermic (increased torpor use, an option not typically available to birds) at cooler high altitudes. Conversely, larger body size in females may be a result of selection for homeothermy during pregnancy (Williams & Findley, 1979) which would require the warmer temperatures of low elevations if food availability is not sufficient to support the higher energetic demands of maintaining normothermia at high altitudes. Thus, while size dimorphism may be an important factor in explanations of both bird and bat altitudinal migration, the ability of bats to use torpor (and the benefits of homeothermy in pregnant females) may have resulted in reversed patterns of sex-biased migration in species with similar patterns of sexual size dimorphism.

A second hypothesis proposed to explain why many males spend the summer at high elevations relies on mate competition. For many populations that hibernate at high-elevation sites, mating occurs at hibernacula (associated with a behaviour known as ‘swarming’; Fenton, 1969; Piksa, 2008; Piksa *et al.*, 2011). Males remaining at high elevations throughout the summer may gain access to females earlier upon return to hibernation sites. This hypothesis seems unlikely to be the sole explanation for sexual segregation as the short distances involved in altitudinal migration are likely traversed rapidly. Males could live at low elevations in summer and merely migrate in advance of females to gain earliest access to females. Using microsatellite markers to assign probability of paternity, Senior *et al.* (2005) demonstrated that *M. daubentonii* pups were more likely to be fathered by males spending summer months at low elevation – a result consistent with mate competition driving male altitudinal migrations. However, given the random and promiscuous mating system of some hibernating species (Thomas, Fenton & Barclay, 1979), it is unclear how early access to females might provide a reproductive advantage. Further research into post-copulatory mechanisms and other factors affecting mating success is required to elucidate further the plausibility of this hypothesis.

A variation of the mate competition hypothesis could explain migration patterns of populations that do not hibernate at high elevations, but migrate latitudinally in addition to altitudinally (e.g. *Lasiurus cinereus* and *Lasionycteris noctivagans* in North America). Some males apparently migrate latitudinally (as do females) but settle at higher elevations upon reaching their summering grounds (e.g. Cryan *et al.* 2000). Mating occurs in the autumn (Kunz, 1982; Shump & Shump, 1982) and we know of no evidence of altitudinal migration in females of these species. Thus, if the males migrate downhill prior to southward migration, they could gain access to reproductive females earlier than would males that summered further south (similar to the

situation described for *M. daubentonii* by Senior *et al.*, 2005). However, some male *L. cinereus* that over-winter in California migrate to ‘certain boreal “islands” in some of the higher mountain ranges’ (Vaughan & Krutzsch, 1954, p. 432), foregoing the latitudinal component of their migratory cycle. Male altitudinal migration in this Californian population is not consistent with the mate competition hypothesis because females are thought to spend the summer elsewhere (Cryan, 2003). One intriguing possibility warranting investigation is that the decision made by males whether or not to migrate latitudinally (potentially permitting early access to mates) may be mediated by individual condition. Under this scenario, only males able to maintain better body condition would migrate latitudinally with the females, while lower-quality males would forego early mating opportunities, migrating altitudinally and saving energy by increased torpor use (as described above). If this is the case, it would present strong parallels (and interesting variations) to white-ruffed manakins where altitudinal migration mediates a trade-off between factors affecting survival and reproduction (Boyle *et al.*, 2011).

A third explanation for variation in strategy between males and females is competition for food (a.k.a., the ‘submissive male hypothesis’; Weller *et al.*, 2009). Under this hypothesis, low elevations provide superior foraging conditions but reproductive females and/or dominant males competitively exclude subordinate males who then are restricted to inferior higher elevations (Menard, 2001; Russo, 2002; Encarnação *et al.*, 2005; Senior *et al.*, 2005). This hypothesis is similar to that proposed to explain the movements of American dippers (Mackas *et al.*, 2010). In both the birds and bats, lower quality individuals are ‘forced’ up to higher elevations, making the best of a bad deal. Although territoriality is rarely documented in bats, and aerial invertebrate prey resources are difficult to defend, lack of research on this topic may contribute to the paucity of evidence for territoriality. It is noteworthy that most bat species for which competition for food is a proposed cause of differential migration also forage in aquatic habitats as do dippers (Leuzinger & Brossard, 1994; Russo, 2002; Encarnação *et al.*, 2005; Senior *et al.*, 2005). Foraging in these spatially restricted aquatic habitats may thus be a trait that leads to competition for food, thereby indirectly shaping migration patterns. Such an explanation may also explain sex biases observed in riparian habitats in British Columbia, Canada (Grindal *et al.*, 1999). An alternative hypothesis that would result in the same observed patterns is that males altruistically remain in sub-optimal habitat, leaving the higher quality foraging sites for pregnant females and juveniles (a.k.a., the ‘facilitating male’ hypothesis; Weller *et al.*, 2009). The promiscuous mating system of swarming bat species (e.g. Thomas *et al.*, 1979) and the limited interactions between males and females that would result from altitudinal segregation imply that such altruistic explanations are unlikely (Wilkinson, 1987).

The food competition hypothesis could act in combination with the mate competition hypothesis. Males summering at low elevations (perhaps having out-competed subordinate

males who were then forced to remain at high elevations) may have access to superior foraging areas. Better foraging could result in better body condition (Russo, 2002; Senior *et al.*, 2005) which may then result in increased mating success when competing with high-elevation males (Senior *et al.*, 2005). However, it remains to be determined whether the increased mating success results from earlier access to females, from better body condition due to superior foraging opportunities, or some other underlying factor that enables them to out-compete subordinate males. A caveat here is that mass differences inferred to reflect body condition between males summering at high and low elevations (i.e. lower mass of bats at high elevations) may result from a facultative and adaptive reduction of body mass functioning to reduce wing loading, thus decreasing flight costs and increasing manoeuvrability (Russo, 2002; Boyle, Winkler & Guglielmo, 2012).

Many testable predictions can discriminate among competing hypotheses for why males often differ from females in their migration patterns. The torpor and energetics hypotheses predict that all males should remain at high elevations in the absence of females. If competition for low-elevation food resources explains male migration patterns, those that migrated to low elevation should arrive at swarming sites in better condition than those that remain at high elevations year-round. The opposite would be true if males remain at high elevation for the energetic benefits of increased torpor use. If competition for food or mates drives downhill migration of some males, we would expect those males to be bigger, older, and competitively dominant over resident males, and these individuals would be expected to sire more young. Conversely, if the advantage of remaining at high elevations is having first access to females arriving at swarming sites, then resident males should sire more young. In a comparative context, we would expect to see either a higher or lower incidence of downhill migration in species with less promiscuous mating systems under mate competition hypotheses with the direction of this prediction depending on whether mating occurs prior to uphill migration or occurs exclusively at high-elevation sites.

(3) Why do tropical bats migrate altitudinally?

Early studies of altitudinal migration in tropical birds noted the predominance of frugivorous and nectarivorous species among those making altitudinal migrations (Skutch, 1969; Stiles, 1988; Hilty, 1997). This observation led to many tests of hypotheses relying on seasonal and spatial availability of food (e.g. Loiselle & Blake, 1991). The same hypothesis has been proposed for tropical frugivorous and nectarivorous bats (Cockrum, 1991; Valiente-Banuet *et al.*, 1996, 1997; Fleming & Eby, 2003; Fraser *et al.*, 2010). Food availability can potentially explain both up- and downhill movements in tropical and sub-tropical bat species that forage year-round. For food to explain bat migration patterns, either the availability of the food resource consumed by the species must vary spatially and seasonally, or the bats’ dietary

requirements must change seasonally with the elevational distribution of those resources differing from one another.

In Costa Rica, Timm & Laval (2000) noted that the seasonal fluctuations of montane bat populations coincided with seasonal changes in abundance of fruit at their study site. Similarly the seasonal abundance of *Sturnira lilium* and *Sturnira erythromos* in the Argentinian Andes coincided with the fruiting of *Piper* and *Solanum* species, fruits common in the diets of these bats (Giannini, 1999). However, thus far, it is not clear if lower elevations (in Costa Rica) or higher elevations (in Argentina) have higher fruit production rates relative to the elevations and the times of year that these bats depart, a key prediction of this hypothesis. If food availability drives altitudinal migration, bats should always move to elevations with higher relative food abundance.

The availability of floral nectar has been hypothesized to shape the migration patterns of *Leptonycteris yerbabuenae*. If food availability drives these migrations, we predict that populations would remain sedentary in areas where food remained available year-round. Furthermore, variation in flowering phenology at different elevations may lead to exclusively altitudinal migrations (with no latitudinal component). Evidence supports both predictions. In Baja California, the flowering of columnar cacti and *Agave* spp. is relatively aseasonal, with many species flowering throughout the winter (Fleming, Nuñez & Sternberg, 1993) and *L. yerbabuenae* are non-migratory in this region (Woloszyn & Woloszyn, 1982; Fleming *et al.*, 1993). Furthermore, several studies have suggested that *L. yerbabuenae* in southern Mexico make altitudinal rather than latitudinal migrations (Valiente-Banuet *et al.*, 1996, 1997; Herrera-Montalvo, 1997; Rojas-Martínez *et al.*, 1999). The hypothesized function of these movements is to track floral abundance as flowering phenology moves up mountain slopes. This explanation is the same as that proposed to explain the altitudinal component of the migration patterns of *L. yerbabuenae* populations reaching the SW USA (Cockrum, 1991).

Although tracking food resources is an intuitive explanation for altitudinal migration, we caution researchers to consider alternative hypotheses. For decades, ornithologists tested predictions of food-based hypotheses in isolation. Yet the manakin system reveals how interactions between climate and dietary needs likely explain these migrations, not only in this species but apparently in whole communities of tropical altitudinal migrants (Boyle, 2011). Recent work from Hawai'i suggests that such interacting effects of weather and food may shape bat altitudinal migrations of *Lasiurus cinereus semotus* (an insectivore). One hypothesis to explain upslope migration during the non-breeding season is that storms limit foraging opportunities for aerial prey. Furthermore, during the non-breeding season males appear to migrate upslope in advance of females, possibly as the (larger) females out-compete the (smaller) males (Menard, 2001). The idea of upslope migration in response to storm-related reduced prey availability is consistent with the fact that on the leeward (drier) side of the island, fewer individuals migrate. Some evidence suggests that upslope migration may also function to

take advantage of seasonal moth irruptions at high-elevation sites (Todd *et al.*, 2009). Even in the absence of irruptive prey, cooler temperatures at high elevations could reduce energy expenditures through use of torpor. Taken together, this relatively simple migration system may combine elements of three hypotheses: limited foraging opportunities (winter storms hinder foraging in lowlands), food abundance (upslope migrations track moth irruptions), and energetics/torpor use at high elevation. Investigations in Hawai'i are ongoing (F. Bonaccorso, personal communication) and we anticipate many novel insights from this migration system.

The patterns of altitudinal migration in the Galapagos Islands are similar to those observed in Hawai'i in several respects. Upslope migration during the breeding season could enable bats to avoid high temperatures and intense rainstorms in the lowlands. It is unclear whether rainstorms might influence migratory movements by limiting the ability of bats to forage for aerial insect prey, or act *via* more direct physiological effects of high temperatures and heavy rain. The pattern of altitudinal sexual segregation in the Galapagos (females low, males high during non-breeding season) is similar to that observed in Hawai'i with the important difference of breeding elevation. In Hawai'i, breeding occurs in the lowlands, and males migrate upslope in advance of females in the post-breeding period (Menard, 2001). By contrast, breeding apparently occurs at higher elevations in the Galapagos, and females migrate downslope during the non-breeding season (McCracken *et al.*, 1997). If the Galapagos females migrate upslope to breed, no clear explanation exists for their return downhill.

V. TAKING BAT ALTITUDINAL MIGRATION STUDIES TO NEW HEIGHTS

This review documents considerable evidence supporting the existence of altitudinal migration of bats. Altitudinal migration putatively occurs in populations living in mountainous regions worldwide (Table 1) and is clearly an important component of the life cycle of many bat species. Also clear, however, is that we have only minimal information on the basic movement patterns of many species, and virtually no hypothesis-driven research investigating the causes and consequences of these migrations. Altitudinal bat migrations appear to be most common in Vespertilionidae and Phyllostomidae. With the exception of one anecdotal report from Nepal, tropical reports are restricted to the New World (likely reflecting variation in research intensity rather than biological patterns given the high proportion of Himalayan bird species that migrate altitudinally). Advancement in this area of research will require creative approaches to both documenting the basic patterns in systems where movements are poorly described, and devising studies that effectively distinguish among the proposed hypotheses that could explain the migrations of better-studied species. Among the species listed in Table 1, wide-ranging species with populations found in non-mountainous regions, where

Table 2. Research efforts necessary to document bat altitudinal migration, the nature of the evidence such efforts would provide, and whether such studies provide information at the population or individual level

Type of research effort	Evidence provided by research effort
Captures/surveys at single elevation, single season	Sex bias (population)
Captures/surveys at single elevation, multiple seasons	Changes in abundance of one or both sexes (population)
Captures/surveys at multiple elevations, single season	Sexual segregation (population)
Captures/surveys at multiple elevations, multiple seasons	Sexual segregation, possibility for detecting temporal variation in migration patterns (population)
Mark-recapture, single elevation	Detailed temporal patterns of arrival and departure (individual)
Telemetry, single elevation	Detailed temporal patterns of timing of departure and possibly direction (individual)
Mark-recapture at multiple elevations, multiple seasons	Confirmed migration of at least the marked individuals (individual)
Isotope studies (claws, fur, wing membrane), single elevation, single season	Equivalent to recapture information for multiple individuals, sometimes possible to estimate range where tissue was grown (individual/population)
Isotope studies, single elevation, multiple years	Temporal consistency in proportion of individuals that migrate (individual/population)
Telemetry, multiple elevations	Temporally and spatially detailed movement information (individual)

These research efforts are listed in ascending order of inferential strength. Some efforts will neither confirm nor refute the occurrence of altitudinal migration, rather simply providing data consistent with the possibility of altitudinal migration. More definitive studies (i.e. greater inferential strength) will provide conclusive evidence.

altitudinal migration is not possible, provide a valuable opportunity for intra-specific comparative studies.

To promote further study, we outline (in ascending order of discriminatory power) methods to document patterns of altitudinal migration (Table 2). These methods can be used to test the predictions outlined in the previous sections to discriminate between the many hypotheses capable of explaining patterns of altitudinal bat migration. Some of the temperate systems (i.e. *Myotis daubentonii* in Europe, *Eptesicus fuscus* or *Myotis lucifugus* in N. America) are ripe for the kind of in-depth investigations recently appearing in the avian literature. In the tropics, most studies must necessarily begin by determining the temporal and spatial patterns of movement before the causes of those movements can be addressed. The predictions included herein are by no means exhaustive, but it is our hope that by identifying connections between observable patterns and underlying drivers, we will encourage more researchers to delve into this wide-open area of study.

Recent technological advances provide several new tools applicable to the study of bat altitudinal migration. Integrating methods such as radio-telemetry and passive integrated transponders (e.g. Neubaum *et al.*, 2006) has enabled detailed and spatially extensive data to be collected on individual animals. Stable isotope analysis is another promising technique that has been used in tropical altitudinal bird migration (Hobson *et al.*, 2003; Boyle *et al.*, 2011), although application of stable isotope methods in bat studies has thus far proven problematic (Fraser *et al.*, 2010). Both isotopes and telemetry allow researchers to document the movement patterns of individuals, information that is critical to providing unequivocal evidence of migration itself, as well as elucidating the drivers of those migrations. Furthermore, many hypotheses lead to predictions involving variation in physiological factors (e.g. body mass, heterothermy,

fuelling rate, energy balance). Therefore, integration of physiological methods into ecological field studies can also greatly expand our ability to distinguish among hypotheses explaining variation in individual movement patterns (e.g. Boyle *et al.*, 2010). Researchers can assess simple body condition indices (Russo, 2002; Senior *et al.*, 2005), or preferably, use respirometry (Cryan & Wolf, 2003), skin-temperature sensitive telemetry (Willis *et al.*, 2006), heart rate telemetry (Dechmann *et al.*, 2011), doubly-labelled water (Butler *et al.*, 2004), and quantitative magnetic resonance (McGuire & Guglielmo, 2010) to test physiological predictions of hypotheses proposed (see above) to explain altitudinal migrations of bats.

Altitudinal bat migration is an important part of the ecology of many species. The IUCN has recognized the need for further investigation of altitudinal bat migration (Hutson *et al.*, 2001). As ongoing climate change pushes montane plant and animal communities upslope, population fragmentation and ultimately the extinction of species dependent upon the highest-elevation habitats is inevitable (Colwell *et al.*, 2008). Not only will year-round residents of high elevations experience the adverse effects of upward-shifting climatic optima and food plant distributions, but altitudinal migrants will likewise find that habitats they depend on for part of their annual cycle have disappeared. When we overlay these climate-related stressors on other threats to bat populations such as habitat destruction and other factors associated with increasing human populations (Hutson *et al.*, 2001), emerging infectious diseases (e.g. white-nose syndrome; Cryan *et al.*, 2010) and other anthropogenic threats (e.g. wind-farm mortality; Cryan & Barclay, 2009), a bleak picture emerges of future bat communities, and indeed, the integrity of many terrestrial ecosystems. Without substantial improvements in our understanding of the patterns and causes of bat migrations, even if those migrations are over short distances

along elevational gradients, conservation strategies for many species will likely prove inadequate.

VI. CONCLUSIONS

(1) Although rarely documented in any detail, altitudinal migration appears to be a common phenomenon in bats around the world. We compiled evidence indicative or consistent with altitudinal migration in 61 species of bats from five families in 21 countries on four continents.

(2) The patterns (and proposed drivers) of altitudinal migration varied biogeographically. In temperate regions, altitudinal migration is sex-biased with females (and perhaps some males) spending the breeding season at low elevations while most (or all) males remain at high elevations. In the tropics, there is no apparent sex bias in most studies.

(3) In some temperate migration systems (e.g. certain populations of *Myotis daubentonii* in Europe, or *Eptesicus fuscus* in North America), the patterns associated with altitudinal migration have been sufficiently documented that it may now be possible to begin testing hypotheses to explain these movements. In the tropics, basic movement patterns have yet to be described in sufficient detail. For both regions, we identified hypotheses proposed to explain migratory movements and we provide testable predictions to discriminate among the various hypotheses.

(4) Comparing bat and bird altitudinal migration systems promises to yield valuable insight into the evolution of complex migration patterns. In some cases, ecological parallels lead to striking similarities (e.g. partial altitudinal migration in bat and bird species that forage in riparian areas) while in other cases, opposite migration patterns are observed despite similar morphology (e.g. partial migration biased towards large-bodied sex in bats and the smaller sex/individuals in birds). Key differences between bats and birds (especially reproductive physiology and thermoregulatory strategies) likely drive many of these patterns.

(5) Effective conservation strategies must include all parts of the annual cycle of migrants. Thus, documenting and understanding altitudinal migration in bats is critical particularly as global climate change leads to shifts in the climatic profile of alpine regions worldwide.

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